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PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON

152nd Session (1939–40) Part 2

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152nd Session (1939–40) Part 2

PROCEEDINGS OF THE GENERAL MEETING
18 January 1940

Mr. J. Ramsbottom, O.B.E., M.A., Dr.Sc., President, in the Chair

The Proceedings of the General Meeting held on Thursday, 23 November 1939, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—John Walter Guerrier Lund.

Certificates of recommendation of the following candidates for Fellowship were read :—For the second time, in favour of Sir Geoffrey Evans, C.I.E., and Walter John Zimmer ; for the first time, in favour of Thornton Horace Hawkins and Richard Clements.

The President reported the deaths of Col. C. J. Bond, Fred Turner, Paul Rosenheim, T. E. James, Dr. E. J. Schwartz, Charles D. Soar, and Arthur R. Thompson, Fellows of the Society.

Dr. T. A. Sprague, F.L.S., gave an account of ' A triploid Aspen—*Populus tremula*—from Sweden '.

Abstract.—

Dr. Sprague exhibited herbarium specimens of a triploid giant Aspen from Tynderö, near Härnösand, Middle Sweden. These were collected in July 1939 during a several days' excursion of the Swedish Dendrological Society, in which Mrs. Sprague and he took part as the guests of Professor and Mrs. R. E. Fries. Full details of this giant Aspen, *Populus tremula gigas*, are given in papers by various Swedish botanists

in 'Hereditas' (XXI, pp. 379–382, 383–393; 1936, and XXIV, pp. 189–194; 1938) and 'Botaniska Notiser' (1937, pp. 119–123, 285) *.

This giant form was first discovered in June 1935 on the Lillö peninsula, Lake Ringsjön, province of Scania, South Sweden. The stand consisted of several hundred trees which had grown from the vegetative multiplication of a single male parent tree. It is accordingly a male clone. The same form was found in July 1936 at Tynderö, Medelpad, Middle Sweden, where there are about twenty half-grown trees averaging 7 m. high. By 1937 the same form had been found in Norrbotten, Northern Sweden.

The somatic chromosome-number of the giant triploid is 57, as compared with 38 in the normal diploid Aspen, *Populus tremula* Linn. The triploid differs from the normal diploid Aspen, found growing beside it, in the larger darker leaves, longer petioles, thicker branchlets, larger buds, and longer stamens. It has broader annual rings, grows much more quickly, and has a considerably larger timber yield than the ordinary Aspen, and has a much higher degree of resistance to attack by *Polyporus*. The trees have a straighter finer growth. The wood of the Aspen is used for making matches and paper, and in the textile industries. Hence the discovery of the giant triploid may be of considerable commercial importance.

The giant triploid is considered to have originated from the union of one reduced and one unreduced gamete. A similar triploid of *Acer platanoides* Linn. has been recorded. Since temperature shocks are known to have produced increase in chromosome number, it has been suggested that the origin of the triploid may have been due to a forest fire.

Discussion.—

Mr. H. W. Pugsley asked whether male plants only had been found in each of the Swedish stations for the triploid.

Dr. Maria Skalinska (Visitor),—Studies of triploids are interesting, as such organisms represent unbalanced caryological types, showing usually a high degree of sterility. Among the living pollen grains sometimes "giant" (diploid) grains can be found. This is the case also in the triploid

* *Addendum.*—According to Bergström in 'Hereditas' (XXVI, pp. 191–201; 20 Jan. 1940), a tetraploid seedling of *Populus tremula* has now been raised by crossing the diploid female type with the triploid male from Lillö. It had larger leaves than any other plant resulting from this cross, but was surpassed in height by some of the approximately triploid seedlings, the vigour ratio of the tetraploid to these being 4 : 4·8.

A number of new triploid aspens, some of which are female, have now been discovered at different localities all over Sweden.

Aspen. In most cases the progeny of the triploids shows the tendency to return to the diploid (or hyperdiploid) number of chromosomes; however, in rare cases it attains a higher, balanced number. In his papers from 1930 and 1932 Müntzing gave detailed studies of a triploid hybrid of *Galeopsis pubescens* × *G. speciosa*, which in its progeny gave only a single plant, a tetraploid, corresponding to the wild species, *G. Tetrahit*. It ought to be added that also in such genera which lack polyploid differentiation in nature, the occasional appearance of a triploid can lead to the production of tetraploids. In my experiments in *Aquilegia chrysantha* × *A. flabellata* (1934) a highly sterile triploid, which appeared unexpectedly in the first hybrid generation, produced chiefly tetraploids in its progeny. In such cases the appearance of a triploid becomes a phenomenon of evolutionary value, as it represents the first step, leading to the formation of a type with a stable higher chromosome number; thus it creates new possibilities for a further differentiation of the genus.

In reply to Mr. H. W. Pugsley, Dr. Sprague stated that the triploid *Populus tremula gigas* of South and Middle Sweden was male, and that the sex of the triploid from North Sweden appeared to be unknown. With reference to Dr. Skalinska's remarks, he mentioned that Swedish botanists were endeavouring to produce a tetraploid by crossing the normal diploid Aspen with the triploid. [See footnote on p. 112, being an Addendum added in press.]

Mr. D. J. Scourfield, I.S.O., F.L.S., gave an account of his paper, 'The oldest known fossil Insect (*Rhyniella praecursor* Hirst & Maulik)—further details from additional specimens. [Printed in full below.]

Mr. A. H. G. Alston, F.L.S., gave an account of 'Notes on the supposed hybrids in the genus *Asplenium* found in Britain'. [Printed in full, p. 132.]

THE OLDEST KNOWN FOSSIL INSECT (RHYNIELLA PRAECURSOR HIRST & MAULIK)—FURTHER DETAILS FROM ADDITIONAL SPECIMENS.

By D. J. Scourfield, I.S.O., F.L.S., F.R.M.S.

In a paper on some arthropod remains from the Middle Devonian Rhynie Chert, Hirst and Maulik (1926) described and figured four heads of a small animal which they believed to belong to the Insecta and which they named *Rhyniella praecursor*. The validity of the assignation of these remains to the Class Insecta was received with some scepticism by

many zoologists, but the late Dr. R. J. Tillyard, after a careful examination of the four specimens, came to the conclusion that, not only were they true insects, but that they definitely belonged to the Collembola (Tillyard, 1928).

Since the publication of these two papers, further specimens have been found in the same material, one by myself (No. 5) and the others by the late Rev. William Cran, but before describing the new specimens it will probably be useful to briefly recall what was known from Hirst and Maulik's and Tillyard's papers.

As pointed out by Tillyard, there were really only two structures in the material then available which were sufficiently well defined to serve as guides to the systematic position of the organism. These were the antennae (referred to in one place by Hirst and Maulik as palp and in another as antenna) and the mandibles. As regards the latter it was clear that they were lodged within the head, that they were elongated, and that they had well-separated molar and incisor areas. These characters in combination suggested that they were Collembolan. Concerning the antennae, they appeared to be definitely four-segmented (the division between the third and fourth segments, however, not so strongly marked as those between the first and second and second and third) with the fourth segment terminating in an oval apex. From these characters and the general proportion of the segments, Tillyard concluded that the antennae were not only Collembolan but even typically Podurid.

The evidence, therefore, from the antennae and mandibles, especially when taken in conjunction with the very small size and the general shape of the heads, made it almost certain that the animals to which the heads belonged were true Collembola and might even be Podurids. Accordingly Tillyard diagnosed the genus *Rhyniella* in the following words :—' A genus of strongly-marked Podurid affinities, distinguished by the form of the mandibles, which have molar and incisor areas strongly separated, almost as in Machilidae, with no definite dentition of the molar area, and by the form of the antenna, in which the distale is only imperfectly divided into third and fourth segments, and is slightly telescopically inserted into the pedicel '.

Nevertheless, so long as no bodies were available, it was still possible to imagine that, considering their great geological antiquity these little heads belonged to animals of some more generalized type than true insects. This question has, however, now been settled, I believe, quite definitely in favour of their Collembolan nature by the discovery of several additional specimens, three practically of heads only, three with head, thorax, and one or two abdominal segments, and a few others,

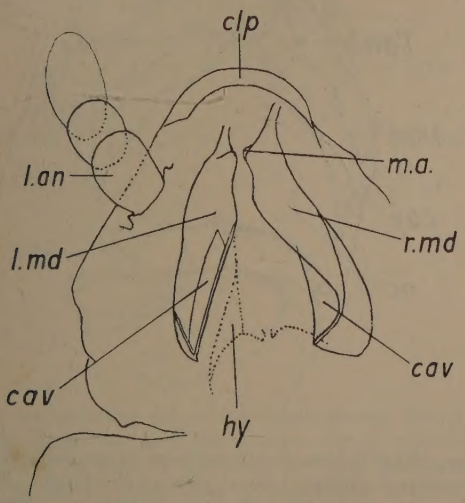
either very obscure or mere fragments. Most unfortunately no specimen has yet been found, notwithstanding prolonged search, showing the posterior abdominal segments. From a consideration of the new specimens and a re-examination of the original four heads the following expanded details can now be given.

Description of *Rhyniella praecursor* Hirst & Maulik.

Head.

Size and general shape.—The length of the head, so far as can be judged from the more perfect specimens, appears to have been from ·3 to ·4 mm., a size which corresponds closely with many recent Collembola and which, as Tillyard remarks, practically precludes a reference to any other group except the early larval stages of larger insects such as the Thysanura. It will be seen from the figures that the shape

Fig. 1.



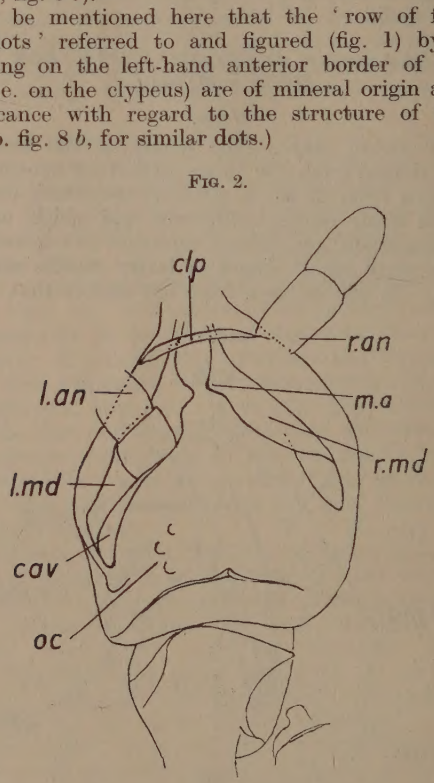
of the head is also very similar to that of many recent Collembola, being somewhat heart-shaped with the pointed end forward.

Clypeus.—This is a most characteristic feature of all the heads. It is not, however, referred to by Hirst and Maulik nor by Tillyard, although it is clearly indicated in three of the figures (A, E, and F) given by the former authors. It

must have been very strongly chitinized, as is the case in some recent Collembola, and well arched. It always appears as a dark brown band and gives the easiest clue to the presence of a head even when the other details are very faint or obscure (see photo, fig. 8 *b*).

It may be mentioned here that the 'row of four small circular dots' referred to and figured (fig. 1) by Tillyard as occurring on the left-hand anterior border of the head-capsule (i.e. on the clypeus) are of mineral origin and are of no significance with regard to the structure of the fossil. (See photo. fig. 8 *b*, for similar dots.)

FIG. 2.

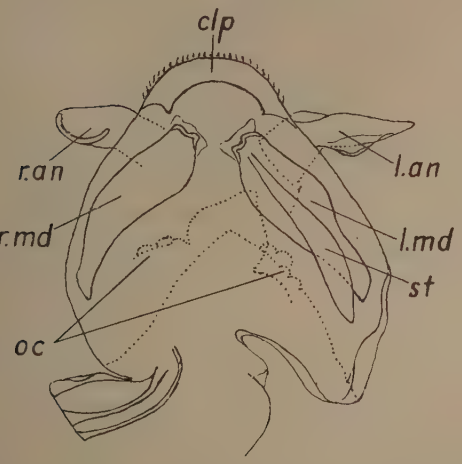


Labrum.—This is best shown perhaps in specimen 6 (fig. 6) *, which presents a slightly lateral view of the head. It appears to have been covered with tufts of delicate hairs. Specimens 5 and 7 also show the labrum beyond the clypeus, but only indistinctly. In specimens 6 and 9 there is a little rounded projection (*r.p.*) just in front of the clypeus, probably one of a pair in each case, and apparently connected with the labrum.

* For convenience of reference the specimens figured in this paper will be alluded to by numbers and the figure numbers will be the same. See list of specimens at end (p. 129).

Ocelli.—In specimen 6 there is a fairly evident group of about six little semicircular lines apparently representing small hemispherical bosses. These structures are slightly behind the insertion of the antenna, on a level with the posterior part of the mandible, and they appear to be on the dorsal aspect of the head. In specimen 10 there are two groups of such circular or partly circular lines (one of six or seven and the other of three), in specimen 3 there are also two groups (one of about three and the other of about four) placed nearly symmetrically on each side of the head, and in specimen 2 there is a small group of about three semicircular lines on one side only. All the lines in these groups,

Fig. 3.



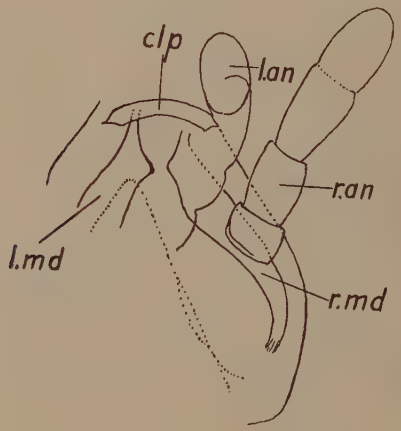
probably representing projecting hemispheres, are of approximately the same size, and the groups occupy more or less the same position as that in specimen 6. This position, namely, posterior to the antennae and on the dorsal surface, together with their shape, makes it almost certain that they represent ocelli. That they appear to vary in number is no doubt due either to the imperfection of the specimens or to the difficulty of making out such small structures in somewhat obscure material lying at various angles. The full number in each group was probably at least six and may have been one or two more. Eight is the maximum number in recent Collembola.

Body-segments.

It seems certain from specimens 5 and 7 that the body-segments were not fused together, that they were subcylindrical, and that they followed the head in a straight line. From this it follows that *Rhyniella* must be classed under the suborder Arthropleona and not under the Symphypleona.

Prothorax.—It also seems fairly clear from specimens 5 and 7 that the prothorax was not well marked, but reduced and without a tergum, for the first pair of legs appear to originate between the head and the rigid segment immediately following, which, judging by the position of the second and third pairs of legs, must be the second thoracic segment. This origin

Fig. 4.



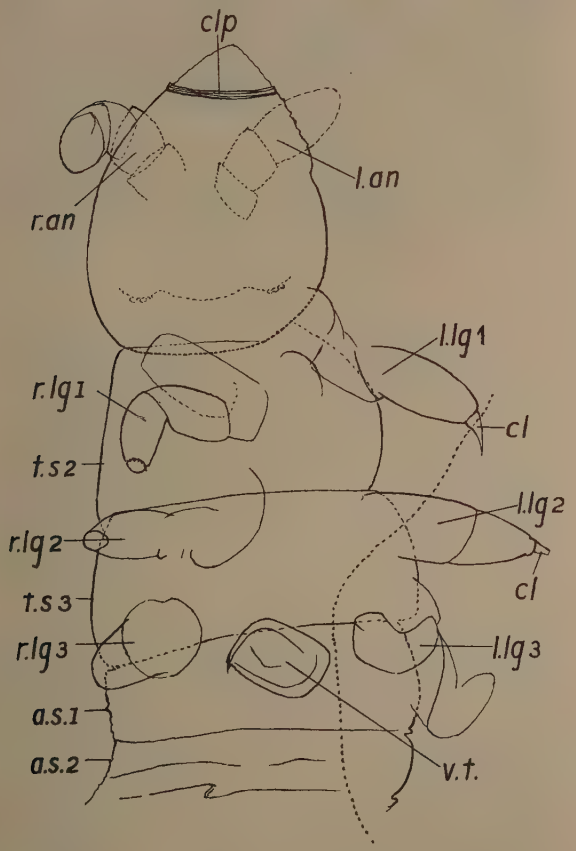
of the first pair of legs from an inconspicuous prothorax is confirmed by specimen 9 which shows a narrow rather ill-defined prothorax with a pair of legs, and also probably by specimens 6 and 8 in which the first pair of legs appear to come out from under the head. This condition of a reduced and probably feebly chitinized prothorax would, taken by itself, bring *Rhyniella* under the family Entomobryidae and not under the Poduridae.

Meso- and metathorax.—These body-segments are very distinctly shown in specimens 5 and 7, which give ventral and side views respectively.

Abdominal segments.—Two abdominal segments are present in specimen 5 and three with part of a fourth in specimen 7. No specimen has been found with the terminal abdominal

segments. This is, of course, very vexing, since the possession of six abdominal segments is considered characteristic of the Collembola, and it also makes it impossible to say whether *Rhyniella* possessed a ' spring ' or not.

Fig. 5.



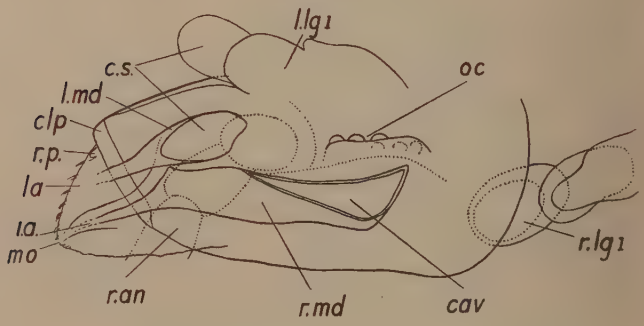
Appendages.

Antennae.—As already stated, it was evident from the originally described specimens that the antennae were four-segmented, although the separation of the third and fourth

segments was not strongly marked. It also seemed fairly evident that the antennae were rather shorter than the length of the head and that the ratio of the lengths of the four segments, reckoning from the basal segment, was round about 4 : 6 : 9 : 8. One detached antenna has been found which confirms these details (fig. 11), and the evidence from the other new specimens, while not conclusive, is in no case inconsistent with them. The same is true also of the oval apex of the last segment. No hairs or other sense-organs have been detected on any of the antennae, but there is a certain irregularity of outline of the apex in the detached antenna and some of the others which may indicate the existence of very minute sensory structures.

Legs and claws.—There can be no doubt that *Rhyniella* had three pairs of legs and no more. This is absolutely clear in specimen 7 and is practically certain in specimens 5 and 9.

Fig. 6.

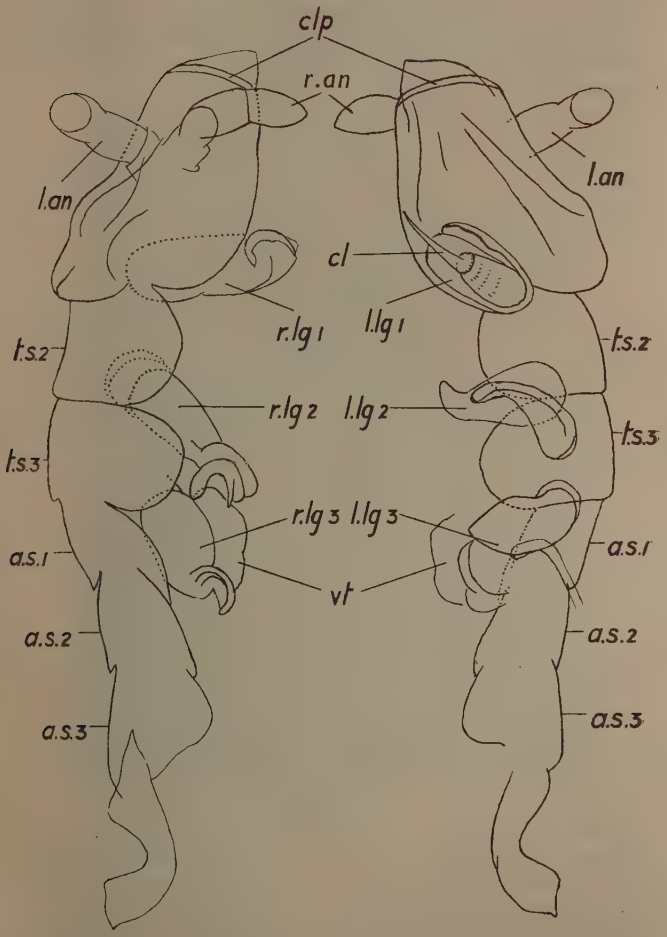


So far as can be judged, they were all similar, but in no case have they been preserved in anything approaching a complete condition, and for that reason the number of segments remains unknown. No doubt each leg terminated in a claw. In specimen 5 there was a complete claw on the left first leg and a proximal part of a claw on the left second leg *. In specimen 7 the left first leg has a complete claw and in specimen 9 there are complete claws on the right first leg and on the right third leg. There is also a claw on a fragmentary specimen lying near to specimen 9. The claws in the three latter specimens are remarkably long and exceedingly delicate. The nearest approach to them in these respects that I have

* A portion of the chip of Rhynie Chert showing these details has, unfortunately, broken away and been lost since the drawing was made. It is indicated by the dotted line in fig. 5.

seen among recent Collembolans are the claws on the first two pairs of legs in *Sminthurides aquaticus*. In specimen 5, to judge from the drawing made before the loss of part of the

FIGS. 7*a* & 7*b*.

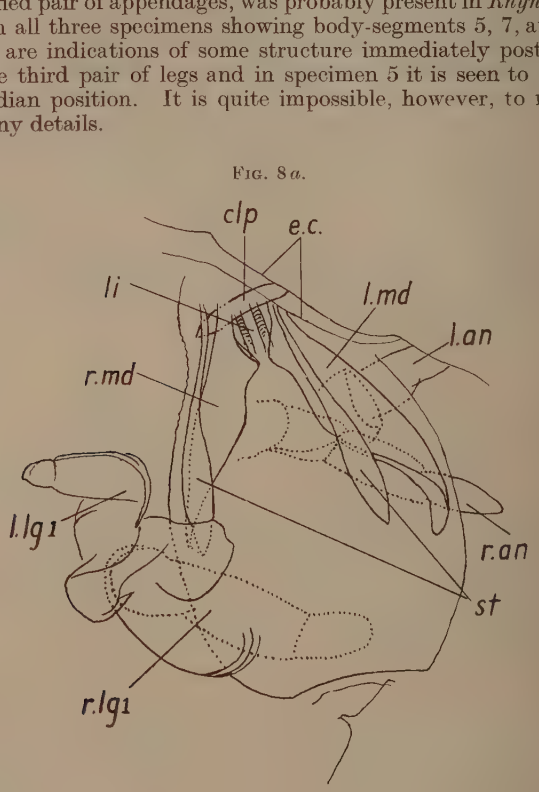


specimen, the claw was shorter and not so delicate. Even if this were actually the case it would still be uncertain whether a specific difference was indicated thereby, for it does not appear

to be associated with any other peculiar characters. In all cases the claws appear to be simple.

Ventral tube.—This structure, usually regarded as a much modified pair of appendages, was probably present in *Rhyniella*, for, in all three specimens showing body-segments 5, 7, and 9, there are indications of some structure immediately posterior to the third pair of legs and in specimen 5 it is seen to be in a median position. It is quite impossible, however, to make out any details.

Fig. 8*a*.



Mouth-parts.

Mandibles.—In each of the four original specimens figured by Hirst and Maulik the mandibles are clearly indicated, and they are undoubtedly present also, in varying degrees of completeness, in specimens 6, 8, 9, and 10 and also probably in specimens 5 and 7, although very difficult to make out. Their essential structure is evident and was described by Tillyard as follows :—' The mandible is much elongated and its distal end is divided into distinct incisor and molar areas. The latter, however, shows no sign of definite teeth, and only

very slight irregularity of the actual grinding surface. This arrangement is evidently a very primitive one, reminding one rather closely of the structure of the mandibles of Machilidae. But the general form of these organs, and in particular their elongation and retracted position within the head-capsule, strongly suggests that they are Collembolan '. To this a few further details may now be added. The incisor area was

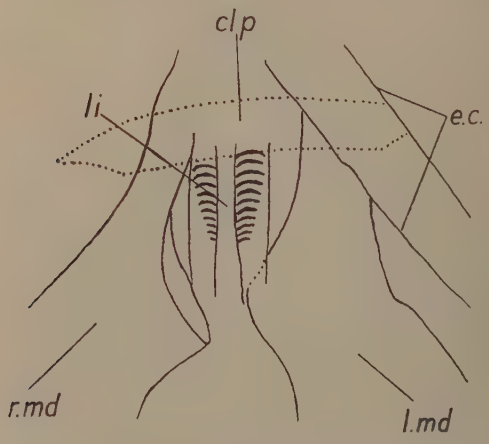
Fig. 8*b*.

apparently rather longer than would be surmised from Hirst and Maulik's and Tillyard's figures and was possibly stylettiform, although the actual apex has not been definitely seen. In any case it is doubtful whether it possessed any teeth. The molar area may have been armed with a few very minute teeth or slight ridges, as, upon a re-examination of specimen 1, it seemed possible to make out a few excessively faint parallel lines in this position on the right mandible. Such lines,

however, have not been seen on any other mandible. The posterior part of the mandible was truncated, appearing rounded at the exterior angle and pointed interiorly, just as in some recent Collembola. There was also a large triangular opening for the insertion of the muscles, with its base at the truncated end and its apex in the somewhat swollen middle part of the mandible.

Maxillae &c.—In several specimens and especially in specimen 8 there is a considerable amount of structure preserved in the head in addition to the mandibles, but the lines are so interlocked that it is very difficult to determine what they represent. With the aid of a little imagination, however, it does seem possible to make out, ventral to the mandibles

Fig. 8*c*.

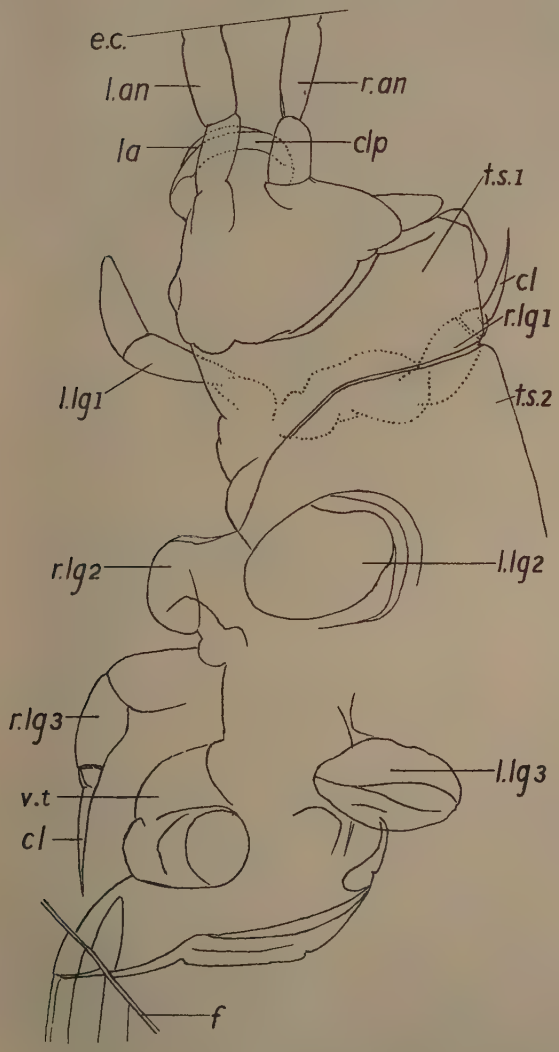


in specimen 8, a pair of fusiform organs pointing towards the mouth. From their position they should represent the 'stipes' of the maxillae, but no indication of the head of the maxillae has been seen. There appears to be a similar structure ventral to the left mandible in specimen 3.

Again, in specimen 8 there are to be plainly seen, just anterior to the molar parts of the mandibles but ventral to these, a pair of straight bands bearing regular slightly curved cross-striae. Their median ventral position suggests that they might possibly be part of a lingua.

There is also a structure in specimen 1, near the left mandible, but more median in position, which Tillyard suggested might be the pedicel of the hypopharynx (=lingual stalk). I have not, however, been able to come to any conclusion about it.

FIG. 9*a*.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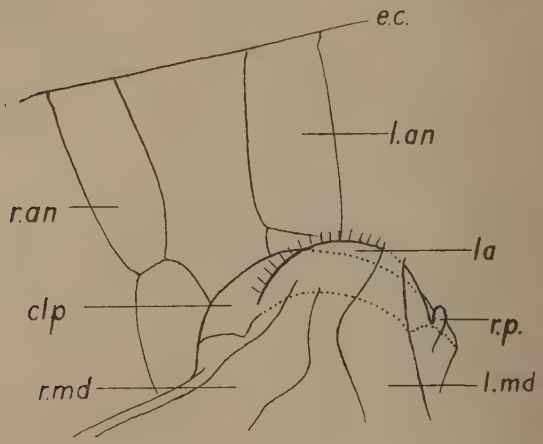
clp
t.s.1
cl
r.lg1
l.lg1
t.s.2
r.lg2
l.lg2
r.lg3
l.lg3
v.t
cl
f

General concluding remarks.

From the foregoing details of its structure, incomplete though they still are and although the full segmentation of the abdomen is not yet known, it would appear that *Rhyniella* was a true Collembolan belonging to the suborder Arthropleona. Within that suborder, however, it seems to have held an intermediate position between the families Poduridae and Entomobryidae. Its antennae were typically Podurid, whereas the absence of a well-developed tergum on the prothorax points to affinities with the Entomobryidae. The excessively long claws, on at any rate two of the specimens, and the possibly stylettiform incisor area of the mandibles are probably

Fig. 9*b*.



not matters of much significance from the point of view of classification, and the same may be said of the undecided question as to whether it possessed a ' spring ' or not. Its size was probably between $1\frac{1}{2}$ and 2 mm. and therefore very similar to many recent Collembola.

In some respects it is very disappointing that *Rhyniella* should not show more characters of a generalized nature and thus throw further light on the affinities of the Collembola or even add something to the elucidation of the vexed question of the origin of insects (see particularly in this connection Calman, 1936 ; Imms, 1936 ; Tillyard, 1930 and 1935). The fact that it does not do so, however, is, nevertheless, very interesting as pointing to the very great antiquity of, at any

rate, the apterygotan insects. The Rhynie Chert, in which *Rhyniella* occurs, is of Middle Devonian age and consequently, according to modern views, some three hundred million years old. But *Rhyniella*, in company with other Collembola,

Fig. 10.

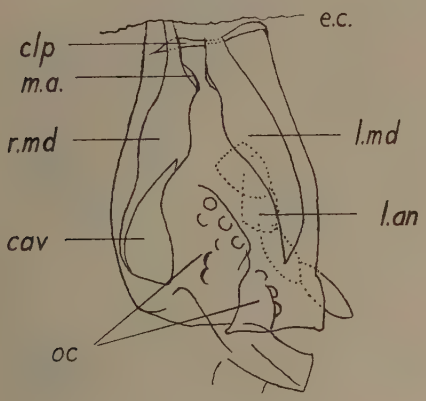


Fig. 11.

although in many ways a primitive type of insect, is also in other ways much specialized, as shown, for example, by the complete withdrawal of the mouth-parts within the head. It follows that the origin of the Collembola, and therefore

presumably, though perhaps not necessarily, of the other apterygotan insects, must be pushed back to some period very much earlier than Middle Devonian.

As regards other records of Collembola as fossils it may be noted that prior to the discovery of *Rhyniella praecursor* the only representatives of the order were those found in amber from the Baltic. These are of many different species, but they all belong to existing genera (Handschin, 1926). This Baltic amber is of Oligocene age. Quite recently, however, another fossil Collembolan has been found in Canada, again in amber, but in this case of Cretaceous age. It has been described by J. W. Folsom (1937) under the name of *Protentomobrya walkeri*, and, curiously enough, it shows the same combination of Podurid antennae with Entomobryid absence of a first thoracic tergum as *Rhyniella*, although in other respects it is very different. It is regarded as belonging to a new family, Protentomobryidae, and it would seem possible that *Rhyniella* could also be placed in this family.

I should not like to conclude without acknowledging my great indebtedness to the late Rev. William Cran of Skene, Aberdeenshire (latterly of Findhorn, Morayshire), who so kindly placed at my disposal all the specimens of *Rhyniella* found by him. My sincere thanks are also due to Dr. W. T. Calman, Dr. A. D. Imms, the late Dr. R. J. Tillyard, and Mr. H. Womersley for their interest and valuable suggestions in connection with this work, and to Mr. J. H. Pledge for photographs of specimen 8, one of which is here reproduced as fig. 8 *b*.

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—— 1930. The Evolution of the Class Insecta. *Papers Royal Soc. Tasmania*, 1930, pp. 1–89.

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List of specimens and figures.

(*Rhyniella praecursor*.)

1. Head : with mandibles and three segments of left antenna. Dorsi-ventral position. Figure dorsal. × 160. H. & M.'s fig. A, T.'s text-fig. 1. Regarded by Tillyard as holotype. (In. 27765 *.)
2. Head : with mandibles and portions of both antennae &c. Dorsi-ventral position. Figure dorsal. × 160. H. & M.'s fig. B. (In. 38225 *a*.)
3. Head : with truncated mandibles, portions of both antennae, ocelli, &c. Dorsi-ventral position. Figure ventral. × 160. H. & M.'s fig. E. (In. 38226.)
4. Head : with mandibles, one complete antenna, &c. Dorsi-ventral position. Figure dorsal. × 160. H. & M.'s fig. F. T.'s text-fig. 2. (In. 38227.)
5. Head, thorax and two abdominal segments : with antennae, portions of three pairs of legs, indication of ventral tube, &c. Dorsi-ventral position. Figure ventral. × 140. (In. 38228.)
6. Head : with mandibles, indications of one antenna, ocelli, &c. Nearly dorsi-ventral position, but slightly to one side. Figure almost ventral. × 150. (In. 38229.)
7. Head, thorax and three abdominal segments : with antennae, three pairs of legs, &c. Lateral position, but head nearly dorsi-ventral. Probably a cast skin. (In. 38230.)
   Figure 7 *a* right side, fig. 7 *b* left side. × 140.
8. Head : with mandibles, antennae, parts of first pair of legs, and much internal structure of undetermined nature (? maxillae, ? lingua, &c.). Dorsi-ventral position. (In. 38231.)
   Fig. 8 *a* ventral, × 160. Fig. 8 *b* photo ventral. × 200. Fig. 8 *c*, ? lingua, ventral. × 550.
9. Head, thorax, and part of abdomen : with parts of antennae, traces of mandibles, three pairs of legs, ? ventral tube, &c. Nearly lateral position, but head nearly dorsi-ventral. Probably a cast skin. (In. 38232.)
   Fig. 9 *a* upper part nearly dorsal, lower part nearly left side, × 140. Fig. 9 *b*, clypeus and parts of labrum, mandibles, &c., ventral. × 270.
10. Head : with mandibles, ocelli, &c. Nearly dorsi-ventral position, but slightly twisted. Figure ventral. × 160. (In. 38225 *b*.)
11. Antenna, detached. × 270. (In. 38233.)

* Registered number in British Museum (Nat. Hist.).

Note concerning the drawing of the figures and the condition of the specimens.

It has not always been possible to insert in the drawings all the details to be seen in the specimens, because of the difficulty of separating and following many of the lines even when fairly well marked or because of the impossibility of showing in a simple line-drawing the passage of a number of structures through different levels. On the other hand, some structures appearing only in an ill-defined manner because of overlying material or some other reason, have had to be represented by sharp outlines.

The specimens are contained in small chips or flakes of Rhynie Chert which are now mounted in Canada balsam on 3″ × 1″ glass slips, but which, for preliminary examination, were simply immersed in oil without any other treatment. As the specimens vary much in their condition of preservation, and are embedded in different degrees in material varying from perfectly translucent to nearly opaque with much extraneous matter, many methods have been used to bring out their details. In some cases a very strong illuminant (e.g. Pointolite) has been essential, but in others a more moderate light has proved preferable. Sometimes a high-power objective with a low eye-piece has been found most useful and in others a lower power with a high eye-piece. Wherever possible, and that is in most cases, the specimens have been examined from both sides of the chip and the details of structure checked in this way.

Explanation of lettering of figures.

an. Antenna.	*lg.* Leg.
a.s. Abdominal segment.	*li.* Lingua (?).
cav. Opening to mandible cavity.	*m.a.* Molar area of mandible.
cl. Claw.	*md.* Mandible.
clp. Clypeus.	*mo.* Mouth.
c.s. Cut by section.	*oc.* Ocelli.
e.c. Edge of chip of chert.	*r.* Right.
f. 'Fault' in chert.	*r.p.* Rounded projection at base of labrum.
hy. Pedicel of hypopharynx (?).	*st.* Stipes of maxilla (?).
i.a. Incisor area of mandible.	*t.s.* Thoracic segment.
l. Left.	*v.t.* Ventral tube.
la. Labrum.	

Discussion.—

Dr. Karl Jordan (Visitor) expressed his great appreciation of Mr. Scourfield's paper, and said that the discovery of the existence of Aptera as far back as the Mid-Devonian was highly important from the view-point of the study of the evolution of insects. The morphology of the recent Aptera had convinced entomologists that these wingless insects

were primitive, and not, like lice and fleas, late derivations from winged forms. An opinion, however well supported by circumstantial evidence, remained in the field of theory and debatable, and might be contradicted by new discoveries. In the present case Palaeontology had confirmed the conviction of the morphologist and turned an opinion into a fact.

Dr. F. E. ZEUNER (Visitor) congratulated Mr. Scourfield on his successes and said that the new material proved beyond doubt that *Rhyniella* belonged to the Collembola. The occurrence of a specialized group of apterygotan insects in the middle Devonian shows that the wingless insects were present long before the winged insects (Pterygota) appeared. The appearance of the latter coincided with the first climax of forest vegetation on the earth. The earliest tree-like plants being middle Devonian, it is conceivable that at that time certain apterygotan insects (which, however, must have been related to the Thysanura rather than to the Collembola) took possession of this new kind of habitat and developed wings from lateral pleurae of the thorax, which acted like a parachute.

Dr. W. T. CALMAN commented on the interest of the glimpse given into conditions when the Rhynie Chert was formed.

Professor F. E. WEISS, in expressing his great interest in Mr. Scourfield's account of *Rhyniella*, drew attention to the fact that the plant-remains found in the Rhynie Chert and described in detail by Kidston and Lang were extraordinarily primitive land-plants in no way directly comparable to any existing groups of plants, while *Rhyniella* apparently could be related to existing Insecta. Similarly, in a later geological period, the Carboniferous, the well-developed insects found in this horizon, could be closely compared with some existing groups of the Insecta, while the plants were essentially different from recent plants. In the evolution of plants as compared with insects there seemed therefore to be a certain lag in the development of modern forms.

The PRESIDENT expressed his appreciation of the patience with which Mr. Scourfield had carried out this most interesting piece of research.

NOTES ON THE SUPPOSED HYBRIDS IN THE GENUS ASPLENIUM FOUND IN BRITAIN.

By A. H. G. Alston, B.A., F.L.S.

While revising the British ferns for a proposed new flora, it has been considered desirable to publish certain preliminary papers, in which doubtful points can be discussed at greater length than will be possible in the flora itself. In this paper the existing statements about supposed hybrids in the genus *Asplenium* are reviewed. The hybrid nature of none of the plants can be considered absolutely proved, and the selection of those to be included in the flora must therefore be more or less arbitrary. However, the evidence is probably as good as that for most of the wild plant hybrids known. In the absence of specimens, figures and descriptions of some of the plants it is naturally quite impossible to reach any satisfactory conclusion.

The best-known hybrid fern is probably the American ×*Asplenosorus ebenoides*, a bi-generic hybrid between *Asplenium platyneuron* and *Camptosorus rhizophyllus*. It has been raised artificially, as described by Miss Slosson (Bull. Torr. Bot. Club, xxix, pp. 487–95; 1902). She placed prothalli of one species with castrated prothalli of the other, and plants morphologically indistinguishable from *Asplenosorus ebenoides* resulted. It is highly desirable that similar experiments should be carried out with the British species.

Besides this method of demonstration there are certain characteristics that hybrids usually possess:—

1. A hybrid is usually intermediate morphologically between the supposed parents. This is, of course, the only evidence that can be obtained from herbarium specimens.

2. It grows with or near the parents: and therefore, when supposed hybrids are discovered, all possible parents growing in the vicinity should be recorded. Exceptions to this rule may occur when hybrids reproduce themselves vegetatively.

3. Complete or partial sterility. This appears to be general among hybrid ferns.

4. Hybrids are usually found as single plants with the parents.

5. Cytological evidence. None has been recorded for these plants, and as they are apparently extremely rare it seems unlikely that any will be available in the near future.

1. ×Asplenium Breynii Retz. Obs. i, p. 32 (1774); Hieron. in Hedwigia, lxi, p. 29 (1919); Bory, Voyage Souterrain, p. 271 (1821).

A. germanicum Weis, Pl. Crypt. Fl. Gött. p. 299 (1770), pro parte, saltem quoad syn. Breynii; Gray, Nat. Arr. ii,

p. 13 (1821) ; T. Moore, Ferns Great Brit., t. xli B (1885) ; Nature Print. Brit. Ferns, Octavo ed., II, p. 126, t. 8 A (1859) ; Hook., Brit. Ferns, t. 27 (1861) ; Lowe, Our Native Ferns, II, p. 159, t. 41 A (1867) ; and in Gard. Chron. N.S. XXIII, p. 80, f. 15 (1885) ; Luerssen in Rabenhorst, Kryptogamen-Fl. Deutschl., ed. 2, III, p. 238, f. 122 (1889) ; Heufler in Verhandl. Zool.-Bot. Ges. Wien, VI, p. 287 (1856) ; Aschers, Fl. Prov. Brandenb., I, p. 915 (1864) ; Laubenberg in Jahresber. Naturv. Ver. Eberfeld, IX, pp. 42–5 (1899) ; F. v. Tavel in Brit. Fern Gaz., VII, p. 49 (1936) ; Murb. in Acta Univ. Lund., XXVII, pp. 1–36 (1892) ; Lowe in Gard. Chron. N.S., XXIII, p. 80 (1885) ; A. D. Webster, in the same, p. 121 ; W. O'Brien, in the same, p. 206 (1885).

? *A. germanicum* var. *acutidentatum* T. Moore, Nature Print. Brit. Ferns, Octavo ed., II, p. 129, t. 80 B (1859).

Asplenium alternifolium Jacq., Misc. Austr. II, p. 51, t. 5, f. 2 (1781) ; Dickson in Trans. Linn. Soc. Lond., II, p. 290 (1794) ; Sm., Engl. Bot., XXXII, t. 2258 (1811), and Johnson's ed. 2, VIII, p. 14, t. 1431 (1841) ; Francis, Analysis Brit. Ferns, p. 49 (1855) ; Bell in Trans. Edinb. Bot. Soc. I, p. 119 (1844). " *A. Ruta-muraria* Auct." ; Newman, Hist. Brit. Ferns, ed. 1, p. 70 (1840), pro parte.

Amesium germanicum Newman, Hist. Brit. Ferns, ed. 3, p. 258 (1864), excl. syn. Weis.

This plant was first recorded from Britain as on ' rocks in the South of Scotland ', by Dickson as *A. alternifolium*. He apparently regarded it as a species. Smith (1811) states that Dickson's locality was ' about two miles from Kelso, on the Tweed ', and adds ' This is, as it were, an intermediate species between A. septentrionale, t. 1017, and A. Ruta-muraria, t. 150, but quite distinct from both '.

Bory de St. Vincent (1821) appears to have been the first to suggest a hybrid origin for *A. Breynii*. He states ' je l'ai rencontrée . . . entre les rochers schisteux du pays de Franchinson, et j'ai de fortes raisons de la croire une hybride de la précédente [A. Ruta-muraria], et de l'Acrostichum septentrionale '.

This view was accepted by certain Continental authors, e.g. Heufler (1856), who pointed out that the spores of *A. Breynii* are usually abortive.

However, a British author, Newman (1840), reduced *A Breynii* to *A Ruta-muraria*, and figured a supposed intermediate from Arthur's Seat, near Edinburgh, while Lowe (1885) considered it a variety of *A. septentrionale*. *A. Breynii* can be distinguished from *A Ruta-muraria* Linn. by its entire indusium.

In 1887 Murbeck found a plant different from *A. Breynii*

which he considered to be the hybrid between *A. septentrionale* and *A. Ruta-muraria*. This was named *A. Murbeckii* by Dörfler in 1895.

Luerssen (1889) pointed out that *A. Breynii* has frequently been found in localities where *A. Ruta-muraria* was absent,

FIG. 1.

A. ×*Asplenophyllitis confluens* (Moore) Alston.
B. ×*Asplenium Murbeckii* Dörfl.
C. ×*A. germanicum* var. *acutidentatum* Moore.
D. ×*A. Breynii* Retz.
E. ×*A. Heufleri* Milde.

and Ascherson (1864) suggested that it was a hybrid between *A. septentrionale* and *A. Trichomanes* Linn.

Laubenberg (1899) also considered it to be a hybrid between *A. septentrionale* and *A. Trichomanes*, because it was always found with those species (often without *A. Ruta-muraria*).

Stansfield and Greenfield (Brit. Fern. Gaz., v, p. 258 ; 1928) state: 'Our own experience was strongly against the idea of *Ruta-muraria* parentage, as in no case did we find it in company with that fern, but always with *septentrionale* and generally with *Trichomanes* not far off'.

In Britain *A. Breynii* always grows with *A. septentrionale*.

Fischer (1909) suggested that *A. Breynii* might be a mutant from *A. septentrionale*.

Heilbron in 1910 produced a hybrid between *A. Ruta-muraria* and *A. septentrionale*, which he states was not the same as *A. Breynii*, but like it. He appears to have been ignorant of the work of Ascherson and Murbeck, so he did not compare it with *A. Murbeckii*, with which it was presumably identical.

According to von Tavel (1936) Dr. Paul Kestner produced *A. Breynii* artificially, by crossing *A. septentrionale* with *A. Trichomanes*. Though the evidence that this plant is a hybrid seems fairly conclusive, it is desirable that Dr. Kestner's experiment should be repeated, and that notes should be made on the species growing with *A. Breynii*.

The name *A. Breynii* has been adopted here instead of *A. germanicum*, because Hieronymus (1919) pointed out that Weis's type-specimen was *A. Ruta-muraria*, a form similar to var. *elata* Lang.

Unfortunately I have not seen Dr. Guétrot's important paper 'Histoire de l'Asplenium (germanicum) Breynii' (in Bull. Soc. Bot. des Deux-Sèvres, pp. 15–31 ; 1916).

Secondary hybrids have been described between *A. Breynii* and *A. septentrionale* (*Hansii* Aschers. and *Luersseni* Waisbecker), and *A. Breynii* and *A. Trichomanes* (*Heufleri* Reich.). There is a specimen of $\times$*A. Heufleri* in Herb. Moore labelled '*A. germanicum anomalum*—Ivery 1866', and another in Herb. Kew labelled '*A. germanicum* var. *obovati-pinnum* Sim, Herb. R. Sim 10/85'. This was probably of German origin and was the variety mentioned by O'Brien (1885). However, *A. germanicum anomalum* Ivery is given as a British fern in Neill Fraser's 'List of British Ferns', p. 1 (1868).

Moore's variety *acutidentatum*, of which there are specimens at Kew, appears intermediate between *A. Breynii* and *A. septentrionale*. It was raised by Sim from *A. Breynii*, and is perhaps the same as one of Waisbecker's 'secondary hybrids'.

Lowe (1885) states that he found every intermediate form between *A. germanicum* and *A. septentrionale* growing from the same root. This was probably one of these 'secondary hybrids'. A. D. Webster (1885) reported a similar plant from Carnarvon, near Bangor, on the Snowdon Range, and another with fronds of both *A. germanicum* and *A. Ruta-*

muraria, on an old wall at Bangor. The latter may perhaps have been ×*A. Murbeckii*. No specimens have been preserved either by Lowe or Webster, and their statements appear to be highly improbable.

2. ×A. Murbeckii Dörfl. in Oesterr. Bot. Zeitschr., xlv, p. 223 (1895).

A. Ruta-muraria var. *cuneatum* T. Moore, Ferns Great Brit., sub t. 41 A (1855); and Octavo ed., ii, p. 124, t. 79 A (1860); Lowe, Our Native Ferns, ii, p. 224, f. 590 (1867), and Brit. Ferns, p. 44 (1890).

A. Ruta-muraria Hook., Brit. Ferns, pro parte, quoad t. 28, ff. 3–4 (1861); non Linn.

? *A. germanicum* (non Weis) T. Butler, Rep. Bot. Exch. Club, 1881, p. 59 (1882).

A. Ruta-muraria var. *pseudo-germanicum* (an Heufl.?) Syme, Engl. Bot. ed. 3, xii, p. 136 (1886), pro parte.

A. Ruta-muraria Linn. × *septentrionale* (Linn.) Hoffm.: Murb. in Bot. Centralbl., xxxi, p. 322 (1887), and in Acta Univ. Lund., xxvii, pp. 36–14, t. 2 (1892): Heilbron in Flora, ci, pp. 16 25, ff. 26, 34 (1910); Rosendahl in Svensk Bot. Tidskr., xii, p. 111, f. 1 (1918); E. Walter in Pterid. Exsicc., p. 29 (1937).

A. germanicum × *perseptentrionale* (non Christ) Rosendahl in Svensk Bot. Tidskr., x, p. 313, f. 3 *a* (1916).

As previously stated *Asplenium Breynii* was originally supposed to be a hybrid between *A. Ruta-muraria* and *A. septentrionale*, but in 1887 Murbeck found another plant which he considered to be this hybrid. A similar plant was raised by hybridization by Heilbron in 1910. In Britain similar plants have been known as *A. Ruta-muraria* var. *cuneatum* T. Moore. Moore's type-specimens agree very closely with the figures published by Murbeck and Rosendahl and with Swedish specimens at the British Museum.

The following specimens are referable to this hybrid :—

Midlothian : Arthur's Seat, *Dr. Lyell* (Herb. Moore).

Perth : Stenton Rock, near Dunkeld, cultivated specimens, *Hort. Chelsea* (Herb. Moore); *G. Wollaston* in Herb. Kew).

A. septentrionale and *A. Ruta-muraria* are both known from Stenton Rock, and *A. septentrionale* from Arthur's Seat.

A supposed hybrid between *A. Ruta-muraria* and *A. Breynii* was mentioned by Kickx (in Bull. Acad. Sci. Brux., 1837, and in the Proc. Bot. Soc. Lond., i, p. 69; 1839).

Moore (1855), says 'specimens similar to this last have been found by Dr. Allchin at Town Malling, Kent, and Miss Wright at Keswick. A still narrower but analogous form has been found by Mr. Wilson in Dovedale, and by Dr. Allchin at Ennis [Co. Clare]'. Moore's specimens from Town Malling, collected

by Dr. Allchin, labelled *A. Ruta-muraria* var. *spathulatum*, are *A. Ruta-muraria*. I have seen no specimens to support the other records, and except for Keswick they appear to be improbable localities for *A. Murbeckii* owing to the absence of *A. septentrionale*.

A. Ruta-muraria var. *cuneatum* has been reduced by some authors to var. *pseudo-germanicum* Heufl., which has been reported from Carnarvon, Pass of Llanberis, *T. Butler*. Butler's specimens at the British Museum are different from ×*A. Murbeckii* and seem to be intermediate between it and *A. septentrionale*.

Syme also reports the var. *pseudo-germanicum* from near Bristol, but this record is not mentioned in White's *Bristol Flora* (1912). Lowe (1867) states, 'found by the Rev. T. Ellacombe of Bitton Rectory, near Bristol, in his immediate neighbourhood'. His figure 590 appears to me too young to be identified; later (1890) he cites, 'Near Bitton [Gloucestershire], Rev. T. Ellacombe', and 'Sizergh, Lake District [Westmorland], J. Crossland'. I have seen no specimens, and owing to the absence of *A. septentrionale*, these are not probable localities for ×*A. Murbeckii*.

I have not seen Dr. Guétrot's paper, 'Histoire d'une fougère hybride de la France' (1936).

3. ×Asplenium Clermontae Syme, Engl. Bot., ed. 3, xii, p. 132, t. 1879 (1886).

×*A. Preissmanni* Aschers. & Luerss. in Allg. Bot. Zeit., i, p. 222 (1895), nomen; Aschers., Syn. Mitteleur. Fl., p. 79 (1896); Hayek in Verhandl. Zool.-Bot. Ges. Wien, lv, p. 13 *c*, fig. (1905).

×*A. Reicheliae* Dörfl. & Aschers. in Verhandl. Bot. Ver. Brandenb., xxxvii, p. xlvii (1896).

A. Trichomanes×*Ruta-muraria* Christ, Farnkr. Schweiz, p. 97, f. 15 (1900).

A. Petrachae Naylor in Trans. Edinb. Bot. Soc. viii, pp. 365–6 (1866), in Herb Boswell: non DC.

This plant was originally found by Lady Clermont, in 1863, growing on the back of a garden-wall with the parents, near Flurry Bridge, Ravensdale Park, Newry (Co. Down): the type is a specimen at the British Museum. It is now extinct. Syme states that *A. Clermontae* was a hybrid between *A. Ruta-muraria* and *A. Trichomanes*, and there appears to be no reason to doubt it.

This hybrid has since been discovered on the Continent, the Continental specimens are, however, larger than the British.

4. ×A. refractum (T. Moore) Lowe, Ferns Brit. & Exot., v, p. 103, t. 35 (1858); T. Moore, Nature Print. Brit. Ferns,

Octavo ed., II, p. 65 (1859) ; and Ferns Nat. Print. sub t. 35 A (1855) ; Hook., Brit. Ferns, ed. 3, p. 165 (1857) ; Malinvaud in Bull. Soc. Bot. France, sér. 4, x, p. 359 (1910).

A. fontanum var. *refractum* (T. Moore) Hook., Spec. Fil., III, p. 193 (1860) ; Lowe Our Native Ferns, II, sub t. 42 B (1867) ; Druery, Brit. Ferns, p. 73, t. 4 (1910) ; Stansfield in Brit. Fern Gaz., v, pp. 99–100 (1925), and VI, pp. 258–259 (1934).

A. ebeneum var. *refractum* T. Moore ex Lowe, Native Ferns, p. 170 (1867).

A. fontanum var. *proliferum* Woll. ex T. Moore in syn.

A. Trichomanes×*A. viride* Wollaston in Brit. Fern Gaz., v, p. 130 (1925).

This plant was described by Moore as a variety, from specimens cultivated at Peper-Harrow Park, Surrey, which were alleged to have been found in Scotland by a person named Filden. It has never been found since. The fronds are longer and narrower than those of *A. fontanum* and have a dark brown rachis.

It has recently been identified by Kestner (in Brit. Fern Gaz., VI, pp. 258–9 (1934), and VII, pp. 19–24 (1935) with ×*A. Pagesii* Litard., a hybrid between *A. foresiacum* and *A. Trichomanes*, which has been found in France and at Brissago near Lake Maggiore (Switzerland). This identification was not accepted by Stansfield (Brit. Fern Gaz., VI, p. 38 : 1934). I have compared specimens and find them quite different. Wollaston (1925) suggested *A. Trichomanes*× *A. viride*, which seems quite absurd, as these are both simply pinnate species.

Stansfield (Brit. Fern Gaz., v, p. 100) suggested that it might be a hybrid between *A. fontanum* and *A. ebeneum*.

Specimens have been seen (Moore type, Hort. Peper-Harrow Park, 1851, *E. Moore* ; Hort. Parker, 1855) at Kew, and have a much lighter rachis and more divided less rigid pinnae, which suggest that the probable parentage was *A. obovatum* ×*Trichomanes*. If it is found again the species growing in the neighbourhood should be carefully noted. There is a specimen at Kew labelled *A. Trichomanes serratum*, from W. C. Carbonell's collection : it does not, however, agree with Lowe's figure of Stansfield's plant.

5. Asplenium Adiantum-nigrum×marinum Druce in New Phytologist, x, p. 323 (1911) ; Blackman in The Vasculum, XXVI, p. 28 (1940).

A. Adiantum-nigrum var. *plumosum* Lowe, Brit. Ferns, p. 165 (1890).

Druce stated : ' At the Lizard it (*A. marinum*) grew close to *A. Adiantum-nigrum* and nearby occurred a remarkable

form intermediate in character, suggesting the hybrid *A. Adiantum-nigrum* × *marinum* '. I have examined Druce's specimens and they appear to me to be immature *Asplenium Adiantum-nigrum*. Miss Blackman's specimens from Pabbay, Barra, were also *A. Adiantum-nigrum*.

Lowe stated (cf. *A. Adiantum-nigrum* var. *plumosum*: ' A grand feather-like hybrid (with *Asplenium marinum*) with deep green fronds. In Mrs. Grant's collection '. No specimens have been seen, and the evidence appears insufficient to accept Lowe's plant as a hybrid.

6. Asplenium Trichomanes × viride Stansfield in Brit. Fern Gaz., IV, p. 3 (1919).

Westmorland: Levens Park, Kendal, *W. Wilson*.

No specimens of this supposed hybrid have been seen, and the evidence appears insufficient at present.

I propose to deal next with the question of hybrids between *Phyllitis Scolopendrium* and various species of *Asplenium*. Two of these appear to have some claim to be accepted, and for these I propose the name **Asplenophyllitis**.

> Genus hybridarum inter Phyllitidis et Asplenii species, structura intermedium, soris nonnullis scolopendriformibus vel athyrioidiis atque aliis asplenioidiis intermixtis.

These hybrids are analagous to the American × *Asplenosorus ebenoides* (R. Scott) Wherry, the hybrid between *Asplenium ebeneum* and *Camptosorus rhizophyllus*, one of the best-known hybrid ferns. *Camptosorus* is a segregate from *Phyllitis*.

7. **Asplenophyllitis confluens** (T. Moore), comb. nov.

Asplenium Trichomanes var. *confluens* T. Moore ex Lowe, Our Native Ferns, II, p. 207, f. 560 (1867), and Brit. Ferns, p. 36 (1890); Jones, Nature Prints, ser. 3 (1877); Druery, Brit. Ferns, p. 77, f. 38 (1910); Hans in Amer. Fern Journ., VI, pp. 37–39, t. 4 (1916); Stansfield, in Brit. Fern Gaz., V, p. 176 (1927).

A. Trichomanes var. *Willisonii* Lowe, Our Native Ferns, II, p. 213 (1868).

A. Trichomanes var. *hybridum* Lowe, Brit. Ferns, p. 37 (1890).

This plant was first found at Levens Park by G. Stabler, and Lowe (1890) pronounced the Levens Park plant ' an undoubted hybrid probably between *A. Trichomanes* and *A. marinum* ', and added, ' there are no germinating spores, which is the case with the other hybrids '. Druery (1910) added, ' It has been regarded as a hybrid between *A. Trichomanes* and *A. marinum*, but this is doubted, as no *marinum*

grew or was likely to grow in the locality ; hybridization with *Scolopendrium vulgare* is more credible. Similar forms are recorded in four places '. Finally, Hans (1916) raised the hybrid accidentally in a pot in which the two putative parents were growing.

The following records are known :—

Cumberland : Wall of Levens Park, Milnthorpe, Nov. 1865, *G. Stabler* (Herb. Moore).

E. Yorks : Whitby, *W. Willison* (Herb. Moore).

Co. Kerry : near Killarney, in 1875, *P. Niell Fraser* (Herb. Moore).

There are cultivated specimens in the Herbarium of the British Museum from a living plant which I saw in the possession of the late Dr. F. W. Stansfield. There is also a specimen at Kew, labelled ' A. Trichomanes var. illustre Lowe 1875 '.

8. ×**Asplenophyllitis microdon** (T. Moore), comb. nov.

Asplenium marinum var. *microdon* T. Moore, Ferns Great Brit., sub. t. 38 (1855).

A. lanceolatum var. *microdon* T. Moore, Handb. Brit. Ferns, ed. 3, p. 166, f. *b* (1857) ; and Brit. Ferns, Octavo ed., II, pp. 67, 72, t. 69 (1859) ; Lowe, New Ferns, t. 11 B (1862) ; Our Native Ferns, II, p. 154, t. 39 B (1867) ; Jones, Nature Prints, ser. 3 (1877) ; Marquand, Fl. Guernsey, p. 209 (1901) ; Stansfield in Brit. Fern Gaz., v, pp. 14–17, 77 (1923), and VI, p. 33 (1935).

This plant was first found in Guernsey intermixed with *A. obovatum* at some distance from the sea.

Moore (1859) states that ' sori may be found, which are diplazioid, scolopendrioid, or even athyrioid ', characters which could not have been derived from *Asplenium marinum*, but suggest *Phyllitis* as a parent. Col. Jones (1877) considered this plant to be a hybrid between *A. obovatum* * (*lanceolatum*) and *A. marinum*. Stansfield (1923) claimed to have raised some plants of *Phyllitis Scolopendrium* from the spores, and suggested that the parentage was *Asplenium obovatum* (*lanceolatum*) ×*Phyllitis Scolopendrium*.

The following records are known :—

Guernsey : *Miss Mansell* (ex Moore) ; in company with *A. obovatum*, on banks of rough masonry without mortar, *C. Jackson* (Herb. Moore) ; St. Peter's, *Marquand* (ex ipse) ; St. Pierre du Bois, *Miss Wilkinson* (Mus. Brit.).

Cornwall : at village of Gullen (?), 5 miles inland from Penzance, on a ruinous building, with *A. obovatum*, *G. Wager*, 1856 (Herb. Moore).

* The name *A. lanceolatum* is invalid, because it was earlier applied to an Arabian species by Forsskål.

The var. *Sinelii* J. F. Robinson (in Hardwicke's 'Science Gossip', p. 148; 1880) is said to be intermediate between *obovatum* and *microdon*; it was found on old walls near Bagot, Jersey, by Mr. Sinel.

Fig. 2.

A. × *Asplenium refractum* Moore.
B. × *Asplenophyllitis microdon* (Moore) Alston.
C. × *A. Claphami* (Moore) Alston.
D. × *A. Jacksoni* Alston.
E. × *Asplenium Clermontae* Syme.

9. × **Asplenophyllitis Claphami** (T. Moore), comb. nov.

Asplenium lanceolatum var. *Claphami* T. Moore ex Lowe, Our Native Ferns, p. 155 (1867).

This was an accidental seedling in the fernery of Mr. Clapham of Scarborough. It is intermediate between *A. microdon* and *Phyllitis Scolopendrium*.

It is possible that these two are analogous to the so-called secondary hybrids between *A. Breynii* and its parents.

10. ×**Asplenophyllitis Jacksoni**, nom. nov.

Asplenium Adiantum-nigrum var. *microdon* T. Moore, Brit. Ferns, Octavo ed., II, pp. 76, 89 (1860) : Jones, Nature Prints, ser. 3 (1877) ; Lowe, Brit. Ferns, p. 47 (1890).

Originally found in Devon.

Devon : Hartland, 2 or 3 miles inland, on an earthy stone bank, *J. M. Chanter* (Herb. Moore) ; Muddeforth, near Barnstaple, *Jackson* (Herb. Moore) ; near Ashburton, on a bank, 1872, *Jas. Richards* (ex Jones) ; *Miss Bickford* (ex Jones).

Guernsey : *Jackson* (Herb. Moore).

Jersey : Grève de Lecy, Nov. 1863, *E. H. N.* (Herb. Moore).

It was suggested that this was a hybrid between *A. Adiantum-nigrum* and *A. marinum*, but, as it had been found some distance from the sea, this appears to be unlikely. Lowe says an undoubted hybrid and always sterile. Moore states that the sori are ' very frequently scolopendrioid, sometimes diplazioid '. This suggests that *Phyllitis Scolopendrium* would be a more probable parentage than *Asplenium marinum*. There is a cultivated specimen in the Herbarium of the British Museum. Dr. F. W. Stansfield told me that *Phyllitis Scolopendrium* came up in the pot.

A. Adiantum-nigrum var. *subconfluens* Stansfield ex Lowe, Our Native Ferns, II, p. 181, f. 525 (1867), found at Killarney, is rather similar.

11. Ceterach officinarum × Phyllitis Scolopendrium Stansfield in Brit. Fern Gaz. I, p. 46 (1909).

Stansfield states that Lowe ' raised a hybrid between *Scolopendrium* and *Ceterach*, which, unfortunately, did not live long enough to commemorate the achievement '.

Certain presumed hybrids between species occurring in Britain have been found on the Continent, though not yet recorded from Britain. It seems worth while to list them.

12. ×A. Perardi Litard. in Bull. Soc. Bot. Deux-Sèvres, 1909–10, p. 109 (1910).

Asplenium Adiantum-nigrum × *Ruta-muraria* Schinz & Keller, Fl. Schweiz, ed. 3, II, p. 5 (1914).

A. Adiantum-nigrum sub-var. *adianto-rutoides* Pèrard in Bull. Soc. Bot. France, XVI, p. 262 (1869).

×*A. Lingelsheimii* Leymann in Oesterr. Bot. Zeitschr. LX, p. 278, f. 1 (1910).

×*A. murariaeforme* Waisbecker, in Oesterr. Bot. Zeitschr., XLIX, p. 63 (1899).

×*A. Christii* Hahne in Allg. Bot. Zeitschr., p. 103 (1904); non Hieron. (1895).

Recorded from France, Switzerland, Spain, Silesia, Hungary, and Saxony.

This plant has rather the habit of *A. Ruta-muraria*, but the stipes is black at the base.

13. ×Asplenium Souchei Litard. in Bull. Soc. Bot. Deux-Sèvres, 1909–10, p. 100, t. 1, 2, 3 (1910).

Asplenium Adiantum-nigrum × *septentrionale* Schinz & Keller, Fl. Schweiz, ed. 3, II, p. 5 (1914).

×*A. paradoxum* Beauverd in Bull. Soc. Bot. Genève, ser. 2, III, p. 297, cum icone (1911); non Blume.

Found in France: Haute Savoie: above Uquie, Alpes d'Annecy.

Beauverd's plant had the aspect of *Asplenium Adiantum-nigrum* var. *acutum*; it grew with the supposed parents.

14. ×Asplenium dolosum Milde in Verhandl. Zool.-Bot. Ges. Wien, XIV, p. 165, t. 4 (1864); Britten, Eur. Ferns, p. 91, c. fig. (1880–2).

A. wachaviense Aschers. & Graebn. Syn. Mitteleur. Fl., ed. 2, I, p. 125 (1912).

A. Adiantum-nigrum × *A. Trichomanes* Milde, loc. cit.

Originally found with the parents near Merano (Italy), and later in Austria and France.

15. ×A. Woynarianum Aschers. & Graebn. Syn. Mitteleur. Fl., ed. 2, I, p. 126 (1912).

A. Adiantum-nigrum × *viride* Aschers. & Graebn. loc. cit.

Recorded from Steiermarck.

The main object of this paper has been to point out the possible hybrids among the British species of *Asplenium*, in the hope that they will receive further investigation from those able to produce them artificially, and that collectors of British plants will search for specimens and make more careful notes on possible parents than has been done in the past.

Discussion.—

Dr. W. T. Calman criticized the position taken that form when intermediate is evidence of hybridity.

Mr. A. J. Wilmott said that, as a field-botanist, he did not consider that the position was exactly as Dr. Calman had indicated, for the recognition of hybrids in the field depended not only on morphological characters but also on distribution. When one knows, in many different areas, two species and their separate ranges of variation, and then finds in an area where the two are growing together individuals outside either of these

ranges of variation and possessing characteristics of both of the presumed parents, the assumption that these individuals are of hybrid origin is justifiable. These ' guesses ' have often been confirmed, and field-estimates justified, by the artificial hybrids raised in the garden after controlled fertilization. To suggest that hybrids are rarely if ever intermediate between the parents is surely an overstatement: as a matter of probabilities it is likely that the position would prove to be best represented by a ' normal ' curve, the majority being intermediate and an ever-decreasing number being found closer to either parent. He cited—as the most extreme case known to him—an instance from the *Fragaria* cultures made at the John Innes Horticultural Institution by Mr. Backhouse, who had shown him a hybrid family so exactly like the male parent that Backhouse thought he had made some mistake in his note-books until, after self-fertilization had been followed by thorough segregation, he discovered in the hybrid family a single character—colour of style—of the female parent.

Mr. ALSTON put in a plea for fuller field-notes from collectors, and in particular records of associated plants which might be putative parents.

PROCEEDINGS OF THE GENERAL MEETING

1 February 1940

Mr. J. RAMSBOTTOM, O.B.E., M.A., Dr.Sc., President, in the Chair

The Proceedings of the General Meeting held on Thursday, 18 January 1940, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

Certificates of recommendation of the following candidates for Fellowship were read:—For the second time, in favour of Thornton Horace Hawkins and Richard Clements.

Mr. A. W. EXELL, F.L.S., exhibited photographs and specimens of an ' Abnormality of a Foxglove '.

Abstract.—

Mr. A. W. Exell exhibited some photographs (taken by Mr. J. A. Crabbe of the Department of Botany, British Museum) and herbarium specimens of abnormal inflorescences of

Digitalis purpurea Linn. This abnormality was first described by Meissner in 1828. It was figured in the 'Gardeners' Chronicle' in 1850, where the hope was expressed that it might give rise to a double Foxglove resembling the double Stock. In 1911 it was figured in the 'Report of the Winchester College Natural History Society' as a hybrid between Foxglove and Canterbury Bell (?).

Mr. Exell considered this abnormality, which varies greatly in complexity, to be due to suppression of the internodes at the apex of the inflorescence and consequent synanthy involving two or more flowers and producing a monstrous structure resembling an actinomorphic flower.

Discussion.—

Mr. N. Y. Sandwith compared peloria in *Linaria*, remarking it reappears from seed.

Mr. A. H. G. Alston stated that a plant of *Lamium Galeobdolon* with a regular terminal flower has been found by Mr. Sandwith and himself, which came true when transplanted.

The President stated that he had observed how frequently the report of one abnormal occurrence is followed by one or more similar reports, and suggested experimental sowings of seed whenever seed can be obtained.

Mr. Exell replied.

Dr. C. T. Ingold, F.L.S., gave an account, illustrated with lantern-slides, of 'A new chytridiaceous fungus parasitizing *Eudorina elegans* Ehrenb.'

Abstract.—

In Swithland Reservoir near Leicester a chytridiaceous fungus has been observed parasitizing *Eudorina elegans*. The fungus appears to be new. It clearly belongs to the family Rhizidiaceae of the Chytridiales. Its closest ally seems to be *Polyphagus*.

The zoospore encysts on the surface of *Eudorina* and from this encysted zoospore there is developed a sac-like thallus within the host coenobium. Branched and unbranched rhizoidal processes of the thallus make contact with the host cells, a few of which, however, usually remain unattacked so that the host coenobium retains its motility.

Asexual reproduction is by uni-ciliate zoospores produced in an elongated zoosporangium which arises immediately to one side of the original encysted zoospore, and projects from the diseased *Eudorina*. In its shape, in its relatively large size, and in its mode of dehiscence this zoosporangium shows a close resemblance to that of *Polyphagus*.

A spiny, thick-walled resting-spore (zygospore) is produced following a sexual process. In this process two thalli, which

have infected the same coenobium, fuse, and from the fusion cell the zygospore is budded off. Unlike the zoosporangium, the zygospore is formed inside the host coenobium and does not project from it.

It is proposed to call the fungus **Endocoenobium Eudorinae**, gen. et sp. nov., and a full account will shortly be published.

Mr. A. W. Exell asked if it was rare for a coenobium to be infected more than once by the fungus, and whether it had been possible to recognize sexual strains.

The President asked if zygospores had been germinated.

Mr. D. J. Scourfield said that Dr. Ingold was to be congratulated on having been able to follow the life-history of the parasitizing Chytrid so thoroughly, and especially on having traced the formation of the zygospore. He had never seen Chytrids on *Eudorina*, but had seen them repeatedly on other Volvocales such as *Chlamydomonas* and *Chlorogonium*. He had sometimes seen several zoospores attached to the same host-plant, but he had never seen the production of a zygospore. As regards the zoospores of Chytrids he had occasionally found them free-swimming among nannoplankton organisms obtained by centrifuging pond water. They were very minute, often only 2 μ long, being probably the smallest of flagellated bodies apart from bacteria. They were also characterized by the presence of a single highly refractile globule and by the fact that in swimming the long flagellum was held behind, acting as a propeller.

Dr. Ingold replied: (1, to the President.) That so far he had failed to germinate zygospores, although they were being kept in an ice-box and attempts to germinate them were made at intervals. (2, to Mr. Exell.) That sometimes two individuals infected the same coenobium and each developed asexually without fusion; and (3) That he had no evidence of the existence of plus and minus strains.

Mr. K. A. Pyefinch (Visitor) gave an account, illustrated with lantern-slides, of ' The anatomy of **Ophioica asymmetrica**, sp. nov., a Copepod endoparasitic in an Ophiuroid '. (Communicated by Dr. W. T. Calman, C.B., F.R.S., F.L.S.) [To be printed in full in the ' Journal ', Zoology.]

Abstract.—

An account of a new species of endoparasitic Copepod, found within *Ophiacantha imago*. Ovigerous and non-ovigerous females, in each case with males attached, were available for examination. The male and female are almost equally degenerate, no clear indications of segmentation being present. The female bears a series of serpentine processes, but the male, which is closely pressed within the

ventral groove of the female, is simpler in external form. In both sexes the only internal organs developed are the alimentary canal and reproductive organs. The eggs become massed together in groups as they pass out of the female and remain, enclosed within a layer of host-tissue, pressed against the ventral surface. The method of liberation of the embryos and the mode of feeding are obscure.

Dr. W. T. Calman and Mr. R. H. Burne made some comments; Mr. Pyefinch replied.

Mr. I. H. Burkill, Sec.L.S., gave an account of his paper, 'Varthema's corcopal, at one time said to be the papaya, was the fruit of *Garcinia indica*'. [Printed in full, below.]

The President added some comments.

VARTHEMA'S CORCOPAL, AT ONE TIME SAID TO BE THE PAPAYA, WAS THE FRUIT OF GARCINIA INDICA.

By I. H. Burkill, Sec.L.S.

Varthema's corcopal (1510), Thevet's arbor cydoniae magnitudine et foliis cujus fructus corcopal (1554), Scaliger's melo corcopali (1557), Christopher Acosta's carcapuli (1578), and what Dalechamps wrote (1586), based on Thevet, are to be referred to *Garcinia indica* Choisy *.

In the year 1502 Ludovici di Varthema set out from his native Bologna in a spirit of light-hearted adventure and went successively to Egypt, Tripoli, and Syria. At Aleppo he obtained by bribery a place among the mamelukes told off to escort the annual pilgrimage to Mecca, and in Mecca when due to fall in for the return journey he deserted. During the next three years he travelled in the company of Muhammedans in Persia, India, and Malaysia, reached Ternate and returned to India, where, giving his companions the slip (1506), he offered his service and knowledge to the Portuguese at Cochin. This service he rendered for a very short time partly at Cochin and partly at Cannanore. Then, having repatriated himself via Portugal, he wrote an account of his adventures which proved a best seller. It appeared in Italian in 1510, in Latin in 1511, in German in 1515, in Spanish in 1520, in French in 1556, in Dutch in 1563, and

* *Varthema*, Itinerario de Ludouice de Varthema Bolognese, 1510: *Thevet*, Cosmographia, 1554: *Scaliger*, Exotericarum exercitationum liber, 1557: *C. Acosta*, Tractado de las Drogas y Medicinas de las Indias Orientales, 1578: *Dalechamps*, Historia generalis Plantarum, 1587.

in English in 1577 ; and in some languages went to several editions. By it he gave wide circulation to the existence in Malabar of a fruit he called corcopal, but he described it in words too few to convey its identity. The monk, André Thevet, employed as the French king's geographer, passed the description forward in his 'Cosmographia' without addition.

In 1863 the Hakluyt Society published an edition of Varthema's book, wherein on p. 161, G. P. Badger, as editor, suggested *Carica Papaya* for corcopal. But the Papaya, since it is an American plant, could have reached Malabar when Varthema was there only by the most extraordinarily rapid transport ; and, moreover, it was heard of by Linschoten, who spent the years 1583 to 1589 on the Malabar coast, as having in his time reached Malacca from America via the Philippine islands, i.e. it was not to his knowledge then in India, but was travelling round the world in the direction reverse to that in which the earliest adventurers could have taken it. To destroy the error of identifying corcopal with Carica, it is desirable to identify Varthema's plant ; and Acosta comes to the rescue. On p. 356 of his 'Tractado' (and on p. 274 of the Italian translation of 1585) is an illustrated account of a tree called 'carcapuli', which is certainly corcopul' under a slightly different name ; and both are thereby proved to be *Garcinia indica*, Varthema's and Acosta's names being distortions of the Hindustani words kokam phal, i.e. kokam fruit.

Garcinia indica is a common tree about the foot of the Malabar Ghats. Its fruit is picked when almost ripe, ripened in the dark, and then marketed. The pericarp can be eaten and is dried as a substitute for tamarinds. The seeds yield kokam butter, an edible fat traded along the coast. Varthema wrote, the fruit is extremely good eating and excellent as medicine. Had he been a more scholarly writer he would have written the fruit is extremely good eating and the oil of the seeds excellent as medicine.

Between the appearance of Varthema's book and Acosta's, Garcia da Orta had published (1563) his 'Coloquios'. He makes no allusion to kokam butter, and apparently had no use for it in medicine. But when going to press he was asked to insert a colloquy in lighter vein than the rest and did so. In this colloquy Ruano says, 'I should like to try that vermilion fruit those girls are eating', and Garcia replies, 'We call it brindoes. . . . It pleases the taste of many, but . . . it is very sour. Brindoes serve as a dye and are taken to sea to fill the place of vinegar'.

The name Garcia uses is still used in Goa, and is connected with 'bhirand'—a Marathi name of the fruit. It is interesting

that Garcia did not care to call attention to kokam butter. The inevitable consequence of not doing so and of using an entirely unlike local name for the fruit was that no early writer brought his reference to the tree alongside the references of the others. At Goa he was 380 miles to the north of Cochin, where Varthema had been factor.

PROCEEDINGS OF THE GENERAL MEETING ON 15 FEBRUARY 1940

Mr. J. Ramsbottom, O.B.E., M.A., Dr.Sc., President, in the Chair

The Proceedings of the General Meeting held on Thursday, 1 February 1940, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

A certificate of recommendation of the following candidate for Fellowship was read :—For the first time, in favour of Allan Eslick.

Mr. J. D. Macdonald (Visitor) exhibited specimens and gave an account of an ' Unusual occurrence of melanism in a Roller (*Coracias caudatus* Linn.) '.

Abstract.—

The Roller (*Coracias caudatus* Linn.) is distributed in Africa from Somaliland to Angola and Natal. The colour of the breast is a rich vinaceous-lilac, except in the north-eastern limits of its range, where it is greenish-blue. On this difference the latter was described as a separate species, *Coracias lorti* Shelley. It is now regarded as a race of *C. caudatus*, and certain facts indicate that it is not a very stable one. In a series of specimens regularity in the distinguishing greenish-blue coloration is seldom found. It is nearly always mixed with a greater or less quantity of vinaceous-lilac. Further, in regard to birds kept in captivity, the following editorial note appeared in the 'Avicultural Magazine ' for 1926, p. 322 :—'An important discovery with regard to Rollers has been made by Mr. Whitley. He had several specimens of Lort's Roller (*Coracias lorti*) and these have gradually changed colour and become identical with *Coracias caudatus* . . . ' But an even

more curious change has taken place in a captive bird. On 21 December 1939, Colonel Hamerton, prosector to the Zoological Society, sent a specimen of this Roller to the Bird Room of the Natural History Museum with the following note :—' The bird arrived in the Zoo 4½ years ago. So far as I can ascertain it had previously been in Mr. Ezra's collection and he presented it to the Zoo. I do not know what part of Somaliland or Abyssinia it originally came from. Its plumage was apparently of normal type when it came to the Zoo. I can vouch for this, for I was acquainted with the species in the north-west part of Somaliland during my residence in that country. It began to assume a melanistic change in its plumage about four to five months ago. This had no connections with the pathological condition (acute enteritis) which caused its death '.

In the specimen, which is exhibited, it will be seen that there has been an extensive infusion of black into the plumage so that very little of the original coloration is visible.

I have been further informed that the change may have extended over a rather longer period, but did not attract attention. It was only during the last moult that it became obvious. There were no abnormal changes in food or temperature during its life at the Gardens, and it lived under the same condition as several other species in which no melanistic tendencies appeared.

I merely wish to put this case on record and to leave the interpretation of the facts to those who are specially competent to deal with them.

I should like to add, however, that it appears important to remember that in the animal kingdom melanism may be congenital or acquired. The latter form is known among birds, but the former is much less easily authenticated. It is common knowledge that Bullfinches in captivity can be made to go black by being fed on hempseed. Therefore it seems to follow that a disease of the alimentary system and, one assumes, affecting the assimilation of food, may influence the colour of the plumage.

Discussion.—

Miss G. Lister asked if the Roller from Somaliland which had been presented to the Zoo, in normal plumage, and which had become almost black after a few months there, had been given any special diet different from that of the Rollers in neighbouring cages, who had kept their bright plumage ? Hemp-seed, for instance, is known to cause blackening of feathers.

Mr. H. W. Pugsley remarked that he had noticed individual cases of melanism among the wood-pigeons of St. James's

Park, and suggested that it might be due to the conditions of life obtaining round London.

Dr. Malcolm Smith thought that, unless a very complete autopsy was made, it could not be assumed that the melanistic change was not due to pathological conditions.

Dr. L. Richmond Wheeler asked, with reference to the preceding suggestion of pathology, whether the melanic specimen appeared to be as healthy and normal while alive as other specimens living under the same conditions.

In reply, Mr. Macdonald stated that no special diet was given to the ' melanistic ' bird.

Mr. R. H. Burne also spoke.

In the absence through illness of the author, the President read a summary of Dr. K. V. Srinath's paper, ' Morphological studies in the genera *Calceolaria* and *Herpestis* '. [This paper is printed in full, below.]

Dr. Malcolm Smith, Sec.L.S., gave an account, illustrated with lantern-slides, of 'A journey to the interior of Hainan '. [Printed in full, p. 174.]

MORPHOLOGICAL STUDIES IN THE GENERA CALCEOLARIA AND HERPESTIS*.

By Dr. K. V. Srinath, F.L.S.,
India State Scholar.

More than 200 species of *Calceolaria* are at present known, and they are chiefly confined to the Andes of South America, while a few reach as far north as Mexico. A few species are found in the Falkland Islands and New Zealand. In this paper (*cf.* Srinath, 1939) the morphology of *C. mexicana* Benth. is described. This species from Mexico is naturalized in the hills of Southern India.

Materials for the present investigation were collected at Nandi Hills, a small hill station in the Mysore State, South India, and in the Nilgiri Hills : and I wish to express my indebtedness to Messrs. K. Rangasamy and S. B. Kausik, both of the Department of Botany of the Mysore University, for supplementary material while work was in progress. The investigation was carried out in the Botanical Laboratory of the University of London, King's College, under the

* Being Part I. of a thesis accepted for the Ph.D. Degree of the University of London.

guidance of Professor R. R. Gates, F.R.S., whose valuable help and criticism I gratefully acknowledge. The material was collected between 10 a.m. and 2 p.m. on bright sunny days and fixed on the spot. A variety of fixatives was used, comprising Navashin's fluid (McClung, 1929), chrome-acetic-formalin of Karpetschenko and Langlet (Manton, 1932), B.15 (McClung, 1929), and corrosive sublimate-formalin-acetic-alcohol (Chamberlain, 1932). With most of these a pre-fixation in Carnoy was found desirable, especially in the fixation of young flower-buds. An exhaust pump was invariably used to aid proper fixation. For older stages, such as mature ovaries and ovules, formalin-acetic-alcohol (Chamberlain, 1932) and Weinstein's modification of Licent's fluid (Weinstein, 1926) were found to be most suitable. Great difficulty was experienced in sectioning the seeds on account of the hard testa. Prolonged immersion in glacial and 80 per cent. acetic acid made it easier: and immersion in glycerine proved a suitable aid. Most of the buds were sectioned at 12 μ–14 μ and stained with Heidenhain's iron-alum-haematoxylin. While it is customary to differentiate the stain in either 2 per cent. iron alum or a saturated solution of picric acid, both of which were employed, acid alcohol was also tried with some success. In later stages I found that very good and clear preparations could be obtained by differentiating the haematoxylin in iron alum (2 per cent. strength) and then immersing the slides in acid alcohol for a few seconds. The acid could best be used with alcohol of 70 per cent. strength. One advantage of doing this is that it leaves the cytoplasm clean after differentiating in iron alum or picric acid. Either the muddy colour of the iron alum or the yellow tinge of picric acid could be successfully got rid of by immersing in acid alcohol.

Ontogeny of the flower.

The flower appears as a knob-like protuberance in the axil of the bract. The calyx is first differentiated from the mass of cells. Then the terminal axis broadens, on whose surface the primordia of the stamens arise. These are organized from the hypodermal layer of the broadened disc, which now has a definitely separate central dome. The next layer to appear is the corolla, which arises from the outer wall of the anther primordium (fig. 1). At a later stage the cells of the central dome present a uniform outline. It is from these cells that the carpels arise.

In the majority of cyclic flowers the origin of the floral parts is in strict acropetal succession. Deviations from this order are reported in many of the Scrophulariaceae. A similar order of appearance of the floral whorls has been described

by Schertz (1919) in *Scrophularia marylandica*. In *Limosella* Svensson (1928) reports that the appearance of the corolla and anthers is almost simultaneous. The same has been reported in other Scrophulariaceae. The appearance of the petals after the stamens is a character which *Calceolaria* shares with the Primulaceae. From a close examination it is seen that the petals are differentiated from the dorsal surface of the stamen primordia. After the appearance of the calyx there appears to be a considerable delay before the next layer is differentiated.

The epidermis of the placental ridge preserves an even surface. The cells of the epidermis along with three or four layers of sub-epidermal cells soon appear differentiated from the rest of the placenta. The cytoplasm in these cells becomes very dense, with prominent nuclei. Very soon the placenta loses its evenness and becomes wavy in outline, and the identity of the numerous ovules on it can be made out as

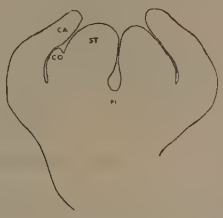


FIG. 1.—Longitudinal section of flower-bud showing the differentiation of the corolla (*co.*) from the dorsal surface of the staminal primordium (*st.*): calyx (*ca.*). The placenta (*pl.*) arises from the mass of cells below the fissure. × 200.

blunt papillae. The ovules do not develop simultaneously, so that a single section often shows various developmental stages of the ovules.

The bicarpellary and bilocular nature of the ovary which is very characteristic of the Scrophulariaceae is not seen so markedly in the genus *Calceolaria*. The ovary is not divided throughout into two compartments, as the separating walls are reduced and are perfectly developed only in the lower part of the ovary. The basal loculi of the ovary hence communicate freely at the top, and the large placenta which is at first roundish, but later ellipsoidal, stands out freely. In order to study the nature of the separating walls in the ovary, a series of cross-sections of the ovary at different levels were examined. It was at once obvious that the development of the septum is very variable. Usually it reaches a

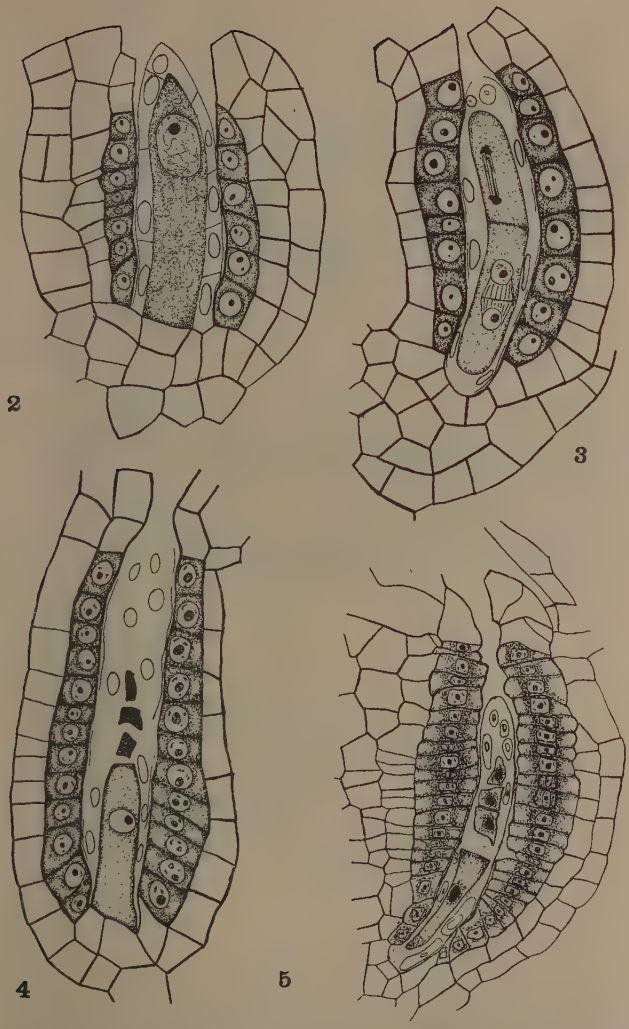
height which corresponds to about a half or a third of the length of the ovary. There appears to be a tendency to ultimate disappearance of the separating wall, resulting in a free central placenta.

The nature of the placenta in the Scrophulariaceae has an important bearing on the question of affinities with the Lentibulariaceae. This family is considered closely related to the Scrophulariaceae by most systematists, and the only conspicuous distinguishing feature is the free central placentation of the former as distinct from the axile placenta of the latter. The presence of intergrading genera such as *Calceolaria*, and perhaps *Limosella*, makes it rather difficult to rely on the nature of the placenta alone to separate the two families. It is necessary to say this because, on the strength of the evidence of a free central placenta alone, attempts have been made by systematists to discredit the close phylogenetic relationship between the two families (Malligson, 1922).

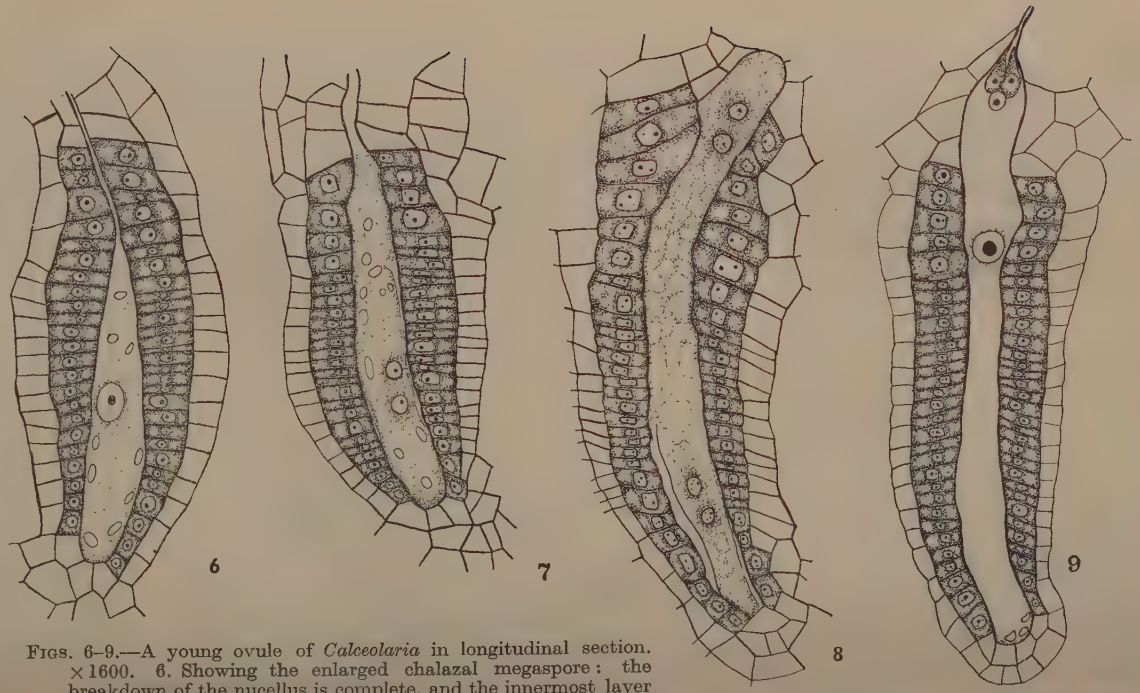
It was pointed out earlier that the ovules appear as undulations on the surface of the placenta. Each papilla is the rudiment of an ovule which grows upwards and becomes at first orthotropous. The archesporium is distinguishable at a very early stage, becoming apparent even before the integument is differentiated. The integument begins in the form of an annular outgrowth from the base of the nucellar tissue. A large hypodermal cell with dense cytoplasm and a large nucleus is soon obvious. This is the single archesporial cell. Only one layer of cells of the nucellus encloses the archesporium at this stage. This hypodermal initial functions directly as the megaspore mother-cell without a periclinal division. The differentiation of the archesporium in the ovule before the initiation of the integuments has been reported in a number of genera, *Digera* (Joshi, 1934), *Carya* and *Juglans* (Langden, 1935), *Hicoria* (Woodroof, 1928). Murbeck found it in the Rosaceae (1901) and Potamogetonaceae (1902). The young ovule grows rapidly while the megaspore mother-cell is elongating. Once laid down, the integument grows rapidly and overtops the nucellus. Due to unilateral growth, the orthotropous ovule gradually becomes bent and assumes its mature anatropous condition. Many of the ovules possess long funicles. This variation in the lengths of the funicle enables the plant to produce a greater number of ovules per unit area of placenta than it would otherwise be able to do.

The nucellus proper does not divide and is composed of a single layer of cells. With the development of the embryo-sac the nucellus begins to degenerate. The bulk of the ovule is composed of the massive integument, as is often the case in the Scrophulariaceae.

A short time before the integument has completed its growth



FIGS. 2–5.—A young ovule of *Calceolaria* in longitudinal section. × 1600. 2. Enlarged megaspore mother-cell in meiotic prophase: the nucellus as a single layer of cells. 3. Telophase of the second meiotic division: the cells of the nucellus have lost their walls and their nuclei are free in the cytoplasm. 4. Degeneration of the three megaspores progressive from the micropylar end. 5. Enlarged chalazal megaspore and the degenerated remains of the upper three megaspores.



FIGS. 6–9.—A young ovule of *Calceolaria* in longitudinal section. ×1600. 6. Showing the enlarged chalazal megaspore: the breakdown of the nucellus is complete, and the innermost layer of the integument with elongated cells lies in contact with the wall of the embryo-sac. 7. At the first mitotic division in the embryo-sac. 8. With 4-nucleate embryo-sac. 9. When fully developed embryo-sac and the two polar nuclei have fused.

the megaspore mother-cell, which is considerably elongated, has entered the meiotic prophase. The cytoplasm of the mother-cell is slightly vacuolated, due perhaps to the rapid elongation. As a result of the meiotic mitoses a normal linear tetrad of four megaspores is organized. When first formed they are all alike in size and contents, but soon the chalazal megaspore begins to enlarge. Progressive degeneration of the others starts from the micropylar end. They degenerate and form a sort of cap at the top of the functioning megaspore (fig. 5).

By the time the megaspore mother-cell is completing the meiotic division the anther-sacs have advanced far in their development, the pollen-tetrads being about to be organized. This shows decisive protandry of the flowers. Figs. 2–9 show the development of the megaspores and embryo-sac. While normally the chalazal megaspore develops into the embryo-sac, due to disintegration of the upper three, occasionally the two terminal megaspores were enlarged up to the uninucleate stage.

The development of the embryo-sac is perfectly normal. The nucleus of the chalazal megaspore, which latter is elongated, divides ; and the resulting nuclei pass one to each pole of the embryo-sac. These nuclei divide twice, thus giving rise to two groups of four nuclei, one at each end of the sac. One nucleus from each group then moves toward the centre ; these two nuclei meet and fuse not far from the egg-cell. Balicka-Iwanowska (1899) found in certain genera of the Scrophulariaceae that the polar nuclei fuse about the middle of the embryo-sac and migrate toward the egg at the time of fertilization. It seems likely that the position at the time of fusion may vary in a single species ; thus in *Pedicularis* Schmid (1906) reports that the polar nuclei may fuse in the upper, lower, or middle part of the sac. The egg-apparatus is normal ; the synergids are pear-shaped with a vacuole at the base of each (fig. 9).

The fully developed embryo-sac is very much elongated, with an enlarged micropylar end gradually tapering towards the chalaza (fig. 9). Its cytoplasm is highly vacuolated. The antipodals are small cells lying at the very end of the embryo-sac. The behaviour of the antipodals is extremely variable in members of the Scrophulariaceae. In forms such as *Linaria* and *Herpestis*, the antipodals persist until the complete formation of the chalazal haustoria. In others, e.g. *Digitalis*, they disintegrate early. In *Calceolaria* they do not remain distinct after fertilization. That the behaviour of the antipodals is variable in a family is obvious from studies on Solanaceae, Campanulaceae, etc.

FIGS. 10–13.—*Calceolaria*. × 400. 10. Double fertilization: one of the synergids is intact. 11. A two-celled embryo-sac: the undivided fertilized egg is seen at the micropylar end: the antipodals are seen degenerating at the chalazal end. 12. The chalazal end of a mature seed in longitudinal section, showing the chalazal haustoria. 13. The micropylar end, showing the micropylar haustoria.

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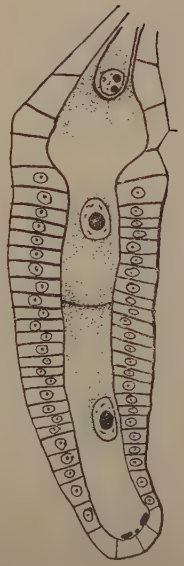

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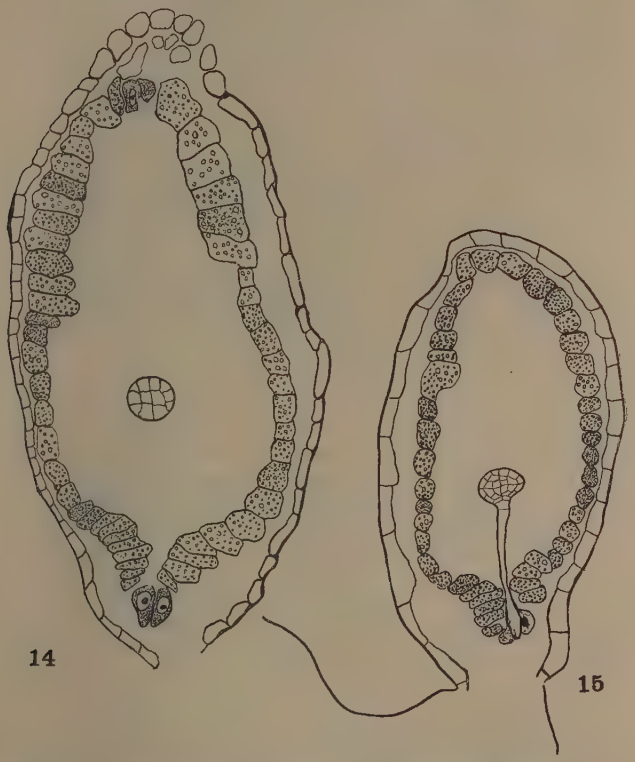
Fertilization.

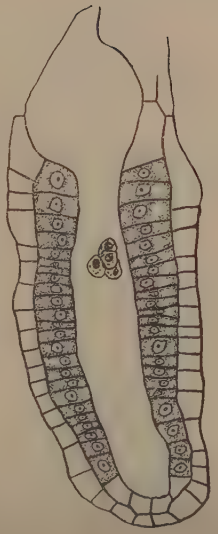
Double fertilization was observed (fig. 10). The pollen-tube enters between one of the synergids and the wall of the sac, as invariably in fertilized ovules one of the synergids is destroyed. The act of double fertilization is perfectly synchronous. The male nuclei tend to be spherical.



Figs. 14 & 15.—The seed of *Calceolaria* in longitudinal section. ×90. 14. Showing the cells of the transformed tapetum and the haustoria at either end. 15. Showing the tip of the suspensor lying amidst the micropylar haustorium.

A long period of rest intervenes after fertilization. The division of the fertilized egg does not take place until the endosperm has attained considerable dimensions. The embryogeny follows the Capsella type. The suspensor is made up of only four cells and disintegrates early. The lower

FIGS. 16–18.—The ovule of *Calceolaria* in longitudinal section. ×400. 16. Showing four antipodal nuclei fusing in the middle of the sac. 17. Before fertilization, showing three nuclei in the middle of the embryo-sac about to fuse and form an endosperm nucleus. 18. Abnormal endosperm development.



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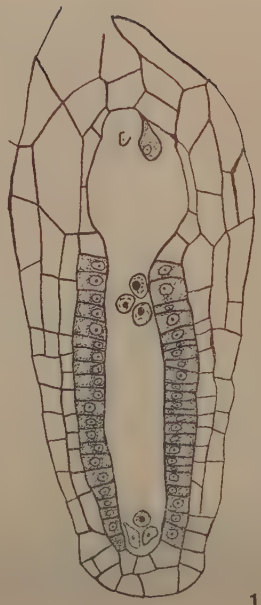

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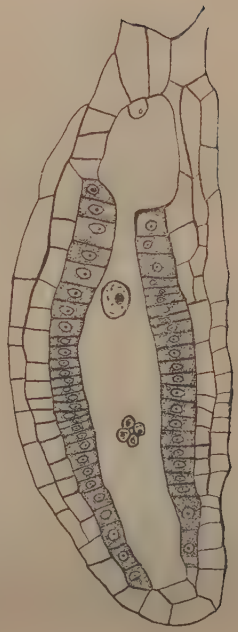

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two cells of the suspensor are rather elongated and sometimes reach the very base of the ovule, almost abutting on the micropylar haustoria (fig. 15). The embryo continues to develop in the normal way to form one of the mature dicotyledonous type.

While usually the endosperm nucleus is the result of two polar nuclei and one male nucleus, cases are known where more than three nuclei fuse (*Peperomia*). The endosperm in these cases would have more than three sets of chromosomes, and the gross chromatin content is necessarily increased. It is difficult to say if this would increase the nutritional value of the tissue. Figs. 16–18 illustrate circumstances which may lead to the formation of an endosperm with more than three sets. In fig. 18 there is a large nucleus in the centre of the sac; and four small nuclei, apparently the four chalazal nuclei, seem to be approaching it.

Discussion.

Nucellus.—In the majority of the Sympetalae the nucellus is made up of a single layer of cells. As development proceeds these cells gradually break down and by the time the eight-nucleate embryo-sac is organized, the nucellus has completely broken down. In *Calceolaria* the disintegration begins just as the chalazal megaspore is enlarging and the upper three breaking down. At this stage, the cells of the nucellus lose their identity and are to be found as loose cells scattered round the embryo-sac. As was pointed out earlier, the cells of the nucellus never divide; they are long and narrow and their transverse walls are usually oblique. This behaviour of the nucellus is usual in other genera of the Scrophulariaceae and has been observed in *Uroskinnera*, *Bartsia*, *Pedicularis*, *Klugia*, *Scrophularia*, etc. In some genera, e.g. *Herpestis* and *Scrophularia*, the elongating embryo-sac pushes its way through the micropylar end of the nucellar layer and when the embryo-sac is formed the nucellus is found surrounding only the chalazal end of the sac. In *Uroskinnera* Balicka-Iwanowska found that the nucellus of the chalazal region persists up to a late stage. *Pedicularis palustris* presents another picture, in which the nucellus of the micropylar zone persists for a long time. Excepting for minor variations, the general rule in most of the Sympetalae seems to be an early disintegration of the scanty nucellus.

Integument.—The history of the integument in the Scrophulariaceae is very interesting. Most Sympetalae have a single massive integument, which is made up of about five to six layers of cells. The innermost layer of the integument undergoes certain marked changes parallel with the development of the embryo-sac. In *Calceolaria* the first sign of any change

is when the megaspore mother-cell is in the meiotic prophase. The cells at this stage are alike in size with the rest of the integument, but their cytoplasm is more densely staining (fig. 2). At the stage when the four megaspores are organized the cells of the integument become more prominent. When the chalazal megaspore is enlarging, the cells of the integument are undergoing a radial elongation followed by repeated longitudinal divisions. As a result the cells become long and narrow compared with the cells of the rest of the integument. This change is completed when the nucellus has completely broken down and the wall of the embryo-sac is in direct contact with the integument. Due to repeated longitudinal division and narrowing, the nuclei of the integument layer become flattened and appear rectangular. The position of the nucleus is central (figs. 4–11) except just before fertilization, when it is near the wall of the embryo-sac. When the layer is fully developed the cells are elongated and palisade-like. In *Calceolaria* this specialized layer invests the embryo-sac completely except at the bulged micropylar end which lodges the egg-apparatus. The changes that this tissue undergoes during the development of the embryo-sac and its contents indicate that it is concerned in the nutrition of the embryo-sac (Srinath, 1938).

The importance of the innermost layer of the integument in the economy of the ovule in general has long been recognized. Numerous names have been given to it by different authors : ' Mantellager ' *i.e.* coat-layer (Jonsson, 1879), ' Endothelium ' (Schwere, 1896), ' Kernhaut ' (Hegelmaier, 1889), ' Embryo-bag envelope ' (Portheim, 1901), ' Epithelium ', ' Tapetum ', Integument tapetum ', ' Couche de Revêtement ', ' Couche epitheliale ', and others.

Westermaier (1897) described a tapetum in *Forsythia Fortunei* and suggested that the tapetum is always separated from the wall of the embryo-sac by a cuticle. Similar observations have been made in the Araliaceae (Ducamp, 1902), in the Scrophulariaceae (Schmid, 1906), *Diospyros* (Longo, 1908), Podostemaceae (Magnus, 1913). All these authors describe the tissue as being composed of cells rich in cytoplasmic content. Hegelmaier (1889) suggested that the function of the ' coat-layer ', as he called it, was a purely protective one. His observations were mainly confined to the Compositae. According to him, the ' coat-layer ' is said to protect the sac from rupturing due to the increased production of endosperm. This idea of protection did not find favour, as is obvious from Goebel's statement (1923).

The only other author who supported the idea of protection was Magnus (1913). He lays stress on the cuticle (' Embryo-dermis '), and claims to have found it also in Campanulaceae,

Dipsaceae, Compositae, Plumbaginaceae, Globulariaceae, and Podostemaceae. He supports Hegelmaier's idea that the cuticle forms an impermeable sheath of high resistance. Both Hegelmaier and Magnus emphasize the importance of the tapetum with its underlying cuticle and interpret its function as one of forming an effective barrier against exudation of the nutritive endosperm from the embryo-sac.

Balicka-Iwanowska (1899), after an exhaustive survey of genera of the Scrophulariaceae, Gesneraceae, Pedaliaceae, Plantaginaceae, Campanulaceae, and Dipsaceae suggested the idea that the modified innermost layer of the integument was primarily nutritive. She was inclined to support Hegelmaier's view that a cuticle is present round the embryo-sac, but that the cuticle is not continuous all round. Goldflus (1898) saw three different layers in the integument of the Compositae, viz. : (1) an outer layer which later on becomes the coat, (2) a middle zone made up of several layers of regular and fairly large cells, (3) the inner layer, i.e. the ' coat-layer ', which is characterized by a dense and strongly staining cytoplasm and by very large nuclei, sometimes becoming a tissue composed of several layers. This author ascribed a digestive function to the ' coat-layer '. Lavialle (1912, 1922), in an investigation of a few genera of the Compositae, confirmed the opinion of Goldflus. Palm (1915) found a particularly well-developed ' coat-layer ', in *Dahlia coronata*, the large nuclei of which had densely staining chromatin. He says : ' In the early stages of development of the embryo-sac—from the mother-cell stage up to its fully developed state—the tapetum serves most probably as an embryonal tissue, the activity of which safeguards the undisturbed growth of the embryo-sac '. This author does not mention the presence of a cuticle. But he suggests that there may be a disintegration of the integument layers outside the ' coat-layer '. Goebel (1923) also is inclined to ascribe a nutritive function to the tapetum.

Schmid (1906), who studied several genera of the Scrophulariaceae, rejects the nutritive nature of the innermost layer of the integument. He considers that the importance of this layer lies in assisting the intercalary growth of the embryo which is practically caught inside the endosperm. The division taking place in the cells of this layer of the integument is said to provide for the increasing size of the embryo and endosperm. This view has met support from several authors : Schnarf (1917, in Labiatae), Glisic (1924, in *Ramondia*), Schnarf (1925, in *Verbena*), Schnarf (1921, in *Klugia*), and Svensson (1925, in *Nemophila*).

The tapetum of the Solanaceae has been studied by a number of authors and has some interesting features. Souèges (1907) demonstrated that a well-developed tapetal tissue is

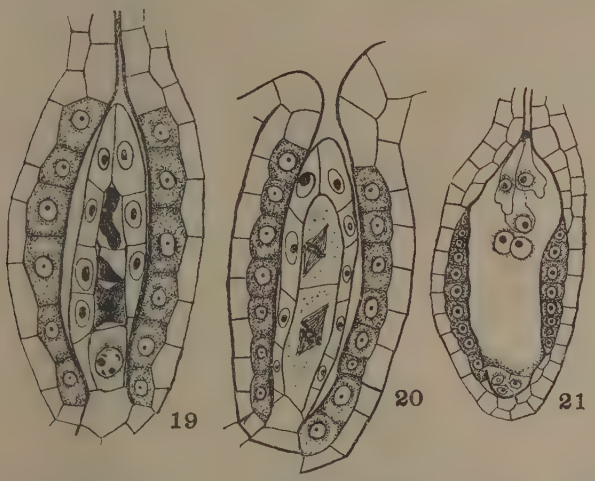
a characteristic feature of this family. He classifies the integument into three distinct zones.

One fact which emerges from the works of earlier authors is the suggestion of a cuticle, separating the integument from the wall of the embryo-sac. After careful examination of the tapetum at different stages of development, I have come to the conclusion that a distinct cuticle does not exist and on *a priori* grounds the existence of a cuticle would be contradictory to the nature of the tapetum. It seems to be highly probable that the earlier authors had confused the crushed remains of the nucellus with a cuticle. At certain stages of development of the embryo-sac the remains of the nucellus closely adpressed to the wall of the integument give an impression that the inner wall of the integument is thicker than the outer wall. The cell-walls of the tapetal cells are of the same size and do not undergo visible changes in structure. That this layer is concerned with the nutrition of the embryo-sac in some way has been suggested by the earlier workers. There seems no doubt about this now. In order to verify this, fresh ovaries were sectioned with a freezing microtome and the sections were tested for starch and proteins, but they were mainly starchy. Free starch has been reported in embryo-sacs of some genera of this family.

The extent of development of the tapetum varies considerably in different families and in the genera of each family. In *Calceolaria* and *Herpestis* the tapetum invests the entire sac except at the antipodal end where a clear differentiation is not obvious. In both cases the swollen micropylar end is free from it. The cells of the tapetum are more elongated and prominent in *Calceolaria* than in *Herpestis*. *Morina longifolia* (Dipsaceae) is the only known plant in which the tapetal tissue completely surrounds the embryo-sac.

A study of the integument in genera of the Scrophulariaceae brings to light the tendency in the ovary to develop a tapetal system capable of nourishing the megaspores and the future sporophyte. So far as function is concerned, the similarity of the embryo-sac tapetum to the anther tapetum is unassailable. In the case of the anther tapetum, the tissue has purely a physiological existence and does not reach the same degree of morphological complexity as in the ovary. The main function of the anther tapetum is to feed the pollen mother-cells at the cost of its cytoplasm. But in the case of the ovary, the integument appears to be specialized to a much greater extent. As I see it, its function seems to be mainly secretory. Mascre (1921) demonstrated that the tapetum of the anther in the Solanaceae secretes a nutritive fluid by a process of karyolysis for the nutrition of the developing pollen mother-cells. It is suggested that the tapetum of the

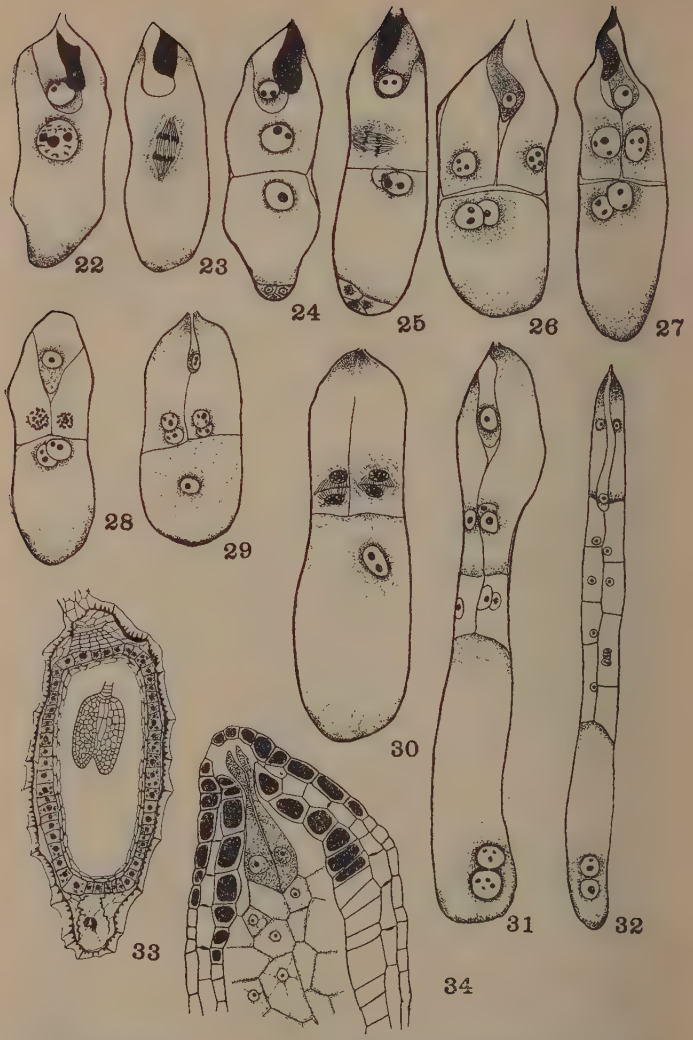
ovary exercises a similar function and contains an enzyme having a digestive function. The integument can be classified into three physiological tracts, the outermost being protective, the innermost secretive, and the intermediate layers for storage. The main function of the tapetum is then to transform the reserve food-materials absorbed from the storage-tracts into a soluble form and then transfer the same to the embryo-sac. Several authors have recorded that the outer layers of the integument break down. I have observed the same in the genera studied, and it seems to be the result of the depletion of their nutritive contents. The activity



FIGS. 19–21.—Ovule of *Herpestis* in longitudinal section. ×1600. 19. Showing a linear tetrad of four megaspores: the chalazal megaspore is enlarging and the upper three are disintegrating. 20. The second meiotic division. 21. The fully developed embryo-sac: the tapetal cells are not elongated as in *Calceolaria*.

of the tapetum as a secretory layer may be said to start from the moment it is brought into contact with the wall of the embryo-sac due to the breakdown of the nucellus. It is generally at the peak of its activity just before fertilization. In later stages the tapetal tract, while losing its nutritive reserves, does not break down but preserves its morphological identity and assumes a protective function in the seed, as will be described.

The endosperm.—In most genera of the Scrophulariaceae the division of the endosperm nucleus takes place soon after fertilization. The secondary endosperm nucleus is slightly



FIGS. 22–34.—*Herpestis*. All × 800, except 31 and 32, which are × 1600. 22. Embryo-sac with the triple fusion nucleus and the fertilized egg. 23. Division of the triple fusion nucleus. 24. Formation of the two-chambered embryo-sac. 25, 26, and 27. Division of the nucleus of the chalazal chamber without wall-formation and the division of the nucleus of the micropylar chamber by a vertical wall, showing the two micropylar chambers and the binucleate chalazal chamber. 28 and 29. Division of the nuclei of the two micropylar chambers. 30. Division of the four micropylar chambers: only two of the spindles are seen in this figure. 31. Later stage showing three chambers in the embryo-sac; the two upper chambers have four cells each and the lowermost chamber is a binucleate cell. 32. Later stage showing divisions

displaced before division, because it is invariably found a little deeper in the embryo-sac when it divides. The exact time of division of the secondary endosperm nucleus is a matter of great variation in different families. There are interesting types where it has been found to have divided even before the fusion of the sperm with the egg-nucleus has been completed: e.g. *Viola* (Bliss, 1912), *Peperomia reflexa* (Fisher, 1914), and *Myosotis arvensis* (Svensson, 1925). There may be a strict synchronization in the time of division of the fertilized egg and the secondary endosperm nucleus, as in the Valerianaceae (Asplund, 1920).

In spite of the great variety of endosperm formation in flowering plants, two broad groups are recognized, viz. (1) free-nuclear endosperm and (2) cellular endosperm. As early as 1856 Hofmeister recognized the existence of these two types. Later, in 1880, Strasburger confirmed this and pointed out that endosperm formation begins either by a free-nuclear division or by the formation of a wall after the first division resulting in a chambered embryo-sac. The latter condition may be said to be the rule in the majority of the Sympetalae. It is also usual to find that the walls laid down after the first few divisions stand in definite directions, having a direct relationship with the form of the embryo-sac. The later divisions are more or less irregular.

The behaviour of the endosperm was studied in *Calceolaria* and *Herpestis*. An account of the details for the genus *Herpestis* will be given first. The first division of the endosperm nucleus is accompanied by a transverse wall dividing the embryo-sac into two halves (fig. 24). The nucleus of the chalazal chamber divides once, but no wall is formed. This binucleate chalazal half of the embryo-sac does not undergo any further change. In later stages this lobe becomes swollen and forms a large bulbous haustorium (fig. 31). The nucleus of the micropylar chamber divides by a vertical wall (fig. 26). A cross-wall is formed by one division again, so that the two longitudinal chambers become four, the upper two being superposed on the lower two. The embryo-sac at this stage is composed of three chambers, the upper two being made up of two cells each and the lowermost one (chalazal) being binucleate. The two upper chambers divide again (fig. 28), so that finally they are made up of four cells each. The four cells at the micropylar end do not divide again, but are transformed into the four prominent micropylar haustoria (fig. 34). The central chamber, by a series of transverse and periclinal divisions, gives rise to a mass of endosperm tissue. From this description it is obvious that only one-third of the endosperm is really nutritive. This nutritive endosperm mass is caught

in the cells of the middle chamber, which form the nutritive endosperm. 33. Showing a late embryo *in situ* and the transformed tapetum: only the chalazal haustorium is seen in this figure. 34. Showing the lobes of the micropylar haustoria.

like an isthmus between the two terminal haustoria. The growing embryo is invariably embedded in this isthmus. The micropylar haustoria, which are made up of four long superposed cells, are very large and have conspicuous nuclei. They are arrow-shaped with blunt ends, which are in contact with the cells of the integument. They appear to be very aggressive and persist even in the seed (fig. 34). But the chalazal haustorium is not active, its cytoplasm becomes granular and the nuclei show signs of disintegration. In the seed stage there is no sign of the chalazal haustorium.

In *Calceolaria* the first division of the endosperm nucleus is accompanied by a wall. The micropylar chamber divides by a transverse wall, so that three chambers are formed, as in *Herpestis*. The endosperm arises from the central chamber. The chalazal chamber divides by a vertical wall and organizes itself into a two-lobed haustorium. A similar change takes place in the micropylar chamber. In *Calceolaria* the central isthmus of the endosperm is connected to either end by haustoria. The chalazal haustoria are more persistent and can be seen in the seed stage (fig. 12). The micropylar haustoria are not conspicuous in the later stages. As the endosperm tissue increases, the embryo-sac grows in size enormously. At the seed stage there is no sign of the cells of the integument, except the innermost layer which functioned as a tapetum. The contents of these cells undergo a gradual change and breakdown. Their walls are thick. In transverse sections of the seed the wall formed by the transformed tapetum has a wavy outline, the thickening not being uniform. The heavily thickened radial walls presumably enable a firm contact to be kept between the neighbouring cells. The breakdown of the contents of these cells is not simultaneous. In very late stages of the seed the cells of the endosperm seem to show a process of degeneration. Those cells in contact with the haustoria are rich in contents, obviously due to the continuous transference of nutrition from the integument by the haustoria. The lignified cells of the tapetum form the heavy testa in the seed. The breakdown of the reserves in these cells is undoubtedly due to the progressive thickening of its walls. The hard testa must be efficient in preventing loss of moisture from the seed.

Apart from rare exceptions, e.g. *Scoparia* and *Moringa*, most of the sympetalous genera have some type of haustorial formation. The embryo-sac itself may form haustorial organs, but discussion of haustoria will be mainly confined to modifications arising from the endosperm. The latter show considerable variation according to whether they arise from a nuclear endosperm or a cellular endosperm. However, haustoria arising from a nuclear endosperm do not show as

high a degree of complexity as do those formed from a cellular endosperm.

The 'basal apparatus' of nuclear endosperms represents the simplest type of haustorial development. In the chalazal end of the embryo-sac of such plants there is usually a considerable increase of cytoplasm containing a large number of free nuclei, which are distinguished from the other endosperm nuclei by their size and staining capacity. The presence of a basal apparatus derived from the endosperm has been reported in a number of plants belonging to different families: *Urtica cannabina*, *U. pilulifera* (Modilewski, 1909*b*), *Polygonum Persicaria* (Woodcock, 1914), *Euphorbia procera* (Modilewski, 1909*a*), *Draba verna* (Vandendries, 1909), *Melilotus alba* (Young, 1905), *Penaea* (Stephens, 1909), *Plumbagella micrantha* (Dahlgren, 1916), *Leptosiphon* (Billings, 1901), *Phacelia tanacetifolia* (Svensson, 1925), *Triglochin maritimum* (Schnarf, 1925), *Xyris indica* (Weinzieher, 1914), *Schizocarpa plantaginea* (Hakansson, 1921), etc. The chalazal part of the embryo-sac is clearly separated from the rest of the endosperm in many of the cases mentioned above. The basal apparatus is an ephemeral organ serving a nutritive function, but takes no part in the formation of the real endosperm. The organization of a basal apparatus causes a quantitative increase of nutrition and renders it in a suitable form for assimilation.

The most striking and well-organized haustoria are found in those endosperms in which walls are formed with the first division of the endosperm nucleus. Almost all these types of haustoria are terminal, i.e. either micropylar or chalazal. A haustorium may be organized at one end of the embryo-sac or at both ends. In a number of genera belonging to the Scrophulariaceae, Labiatae, Plantaginaceae, Gesneraceae, and Hydrophyllaceae, the chalazal cell is distinctly different from the micropylar cell after the first division, which is accompanied by a transverse wall. The formation of cells is partly or entirely suppressed, and the entire cell with its lobe forms a haustorium. In most of them there is one nuclear division, as a result of which the chalazal haustorium is a binucleate cell. It is considerably enlarged and hypertrophied. In the family Scrophulariaceae there are various intermediate types illustrating the evolution of the chalazal haustorium.

A variation sometimes occurs even in the different species of a genus. The species of *Veronica* are very instructive in this respect (Gscheidle, 1924). In the sections Leptandra and Pseudolimachia, two longitudinal walls crossing each other are laid down in the chalazal cell. The four cells thus formed constitute a wedge-shaped haustorium. In the section Beccabunga, an undivided binucleate lobe is formed at the chalazal end. In the section Chamaedrys it has a lateral

branch. Undoubtedly the species with a divided chalazal chamber are more primitive than those with a single chamber. The failure of the lobes to become divided may be a consequence of physiological hypertrophy, i.e. a result of abundance of nutrition, which causes an unusual increase in size. This is very characteristic of glandular organs in general.

Where a chalazal haustorium is formed, a micropylar haustorium may also be formed, but it is always later. The genera of the Scrophulariaceae provide an interesting series of variations in the structure of the micropylar haustoria. In forms like *Verbascum*, *Scrophularia* and *Digitalis*, the micropylar haustorium is made up of four cells. It is two-celled in *Alectrolophus*. In species of *Lathraea* it has either two cells or one four-nucleate cell. In *Veronica*, *Euphrasia*, *Pedicularis*, *Melampyrum*, and *Tozzia* it is regularly a four-nucleate cell. This is the most advanced condition. Haustorial formation in the Lentibulariaceae is very similar to that in the Scrophulariaceae. *Utricularia vulgaris* is an example (Wylie and Yocom, 1923, Kausik, 1935). The chalazal haustorium is binucleate. Here both the micropylar and the chalazal haustoria are extra-ovular, the former sometimes reaching the placenta. The micropylar haustoria in a few genera of the Labiatae, e.g. *Stachys*, *Satureia*, *Brunella*, and *Salvia*, behave in a similar fashion. In *Arisaema triphyllum* (Pickett, 1913, 1915) a mass of leucoplasts are crowded round the nucleus of the chalazal haustorium.

Billings's account (1901) of the haustorial development in *Globularia cordifolia* is remarkable. Terminal haustoria are first formed which would correspond to those that occur in the Scrophulariaceae. The micropylar haustorium grows out of the micropyle and develops four—later more—filiform extra-ovular protuberances. The chalazal haustorium develops a lateral offshoot. At a later stage, when the primary haustoria have ceased their activity, the central endosperm develops protuberances which grow down into the tissue of the chalaza. Such secondary haustoria are rare.

In general, the function of the haustorium is to absorb and transfer nutrition to the developing embryo. The abnormal shapes assumed by the haustoria in certain genera are doubtless the effect of hypertrophy. These haustorial developments reveal that inside the ovule there is a certain degree of autoparasitism. During the development of the gametophyte, we first find that the megaspore which grows does so at the expense of the other three ; the embryo-sac as a whole later grows at the expense of the nucellus and the embryo grows at the cost of the endosperm. This type of autoparasitism in the development of a seed is really remarkable.

The account of the changes that take place inside an ovule from the early stages up to the formation of the seed gives

an insight into the ways in which the problem of nutrition is solved. The highly differentiated tapetum is concerned with this task up to the time of formation of the endosperm. It was pointed out above that the integument in the Scrophulariaceae is more or less physiologically differentiated into three tracts. In the female gametophyte where no special organs are developed, the function of digestion and absorption is distributed over the entire surface of the embryo-sac. Differentiation starts in the tissues, which leads to a distribution of the functions concerned with nutrition. That this is the trend of evolution in the female gametophyte is obvious from a study of the Scrophulariaceae.

The way in which nutrition is provided to the embryo calls for attention. The embryo does not receive its nutrition directly from the mother-plant. Between the two a peculiar tissue is placed which in constitution is neither gametophytic nor sporophytic. This tissue is capable of transforming the nutrition into a suitable form. There is no doubt that the endosperm has a dual rôle. In the early stages it functions as a nourishing organ ; when the development is completed it becomes a storage organ. It is possible to regard the haustoria as nothing but hypertrophied formations under the influence of abundant nutrition. Direct observation clearly indicates that the haustoria absorb nutrition and transfer it to the endosperm. Where parts of the haustoria are extraovular, it is obvious that the contents of cells outside the sac are absorbed. One of my preparations seems to suggest that the suspensor of the embryo lies amidst the micropylar haustorium (fig. 15). This may mean that the nutrition gathered by the haustoria is passed along the suspensor.

Summary.

(1) In the ontogeny of the flower of *Calceolaria* the order of development is calyx, stamens, corolla, and pistil. The corolla arises as an outgrowth on the primordium of the stamen.

(2) The flower is reduced from an original pentamerous plan, two of the sepals and petals showing a strong tendency to fusion. Only two anthers are found.

(3) The incomplete nature of the septum in the ovary confirms the long-assumed but often disputed relationship of the Lentibulariaceae and the Scrophulariaceae.

(4) The megaspore mother-cell forms an axial row of four potential megaspores ; the embryo-sac, of normal type, arises from the chalazal one, while the other three degenerate.

(5) The single-layered nucellus disintegrates early, so that the innermost layer of the single integument lies next to the wall of the sac ; this layer is organized into a nutritive tapetum.

(6) Double fertilization has been observed, the pollen-tube entering between one synergid and the wall of the embryo-sac.

(7) The first division of the secondary endosperm nucleus is accompanied by wall-formation. The lower half of the sac organizes itself into a two-celled chalazal haustorium. The upper chamber is divided into two halves by a transverse wall ; the uppermost chamber develops a two-celled micropylar haustorium ; the central cell develops the nutritive endosperm in which the developing embryo is embedded. The chalazal haustorium is more persistent and is seen at the seed stage.

(8) The embryo follows the Capsella type of development.

(9) The mature seed consists of an embryo surrounded by thickened endosperm-cells greatly gorged with nutritive materials, some of which show signs of degeneration. The inner coat of the seed is formed by the integumentary tapetum which has unequally thickened walls.

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A JOURNEY INTO THE INTERIOR OF HAINAN.

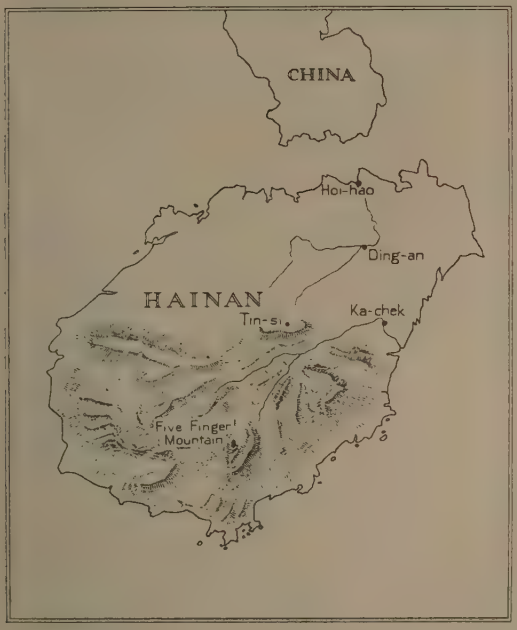
By Dr. Malcolm Smith, Sec.L.S.

The island of Hainan lies at the extreme north of the Gulf of Tongking, and is separated from the mainland of China by a shallow strait some 15 kilometres across at its narrowest part. Roughly speaking the north-eastern half of the island is an undulating plain, the southern and western part is mountainous. This configuration of the country, as will be shown later, is intimately concerned with the fauna and flora of the country.

In 1923, my wife and I, accompanied by two trained native collectors, made a journey into the interior, our main object being to collect zoological and botanical specimens. The great attraction of the visit lay in the fact that the fauna and flora of the island were at that time practically unknown. Our main objective was the Five Finger Mountain, the highest peak of the island.

Landing at Hoi-hao, the port of Hainan, on 7 January, we spent a few days in exploring the neighbouring country and in collecting information for our journey. We could get little that was of any help to us. There was no map of the country ; there were no roads, and as far as the Five Finger Mountain was concerned, no European had ever visited it.

From Hoi-hao we travelled to Ka-chek, a large town near the south-east coast and situated on the edge of the mountainous country. The journey took four days, the first part being made by boat. The country was not particularly interesting ;



it was for the most part treeless and covered mainly with short grass. Villages were small and infrequent, the sandy and rocky nature of the soil preventing much cultivation. Two conspicuous species of birds, that followed us all day in flocks through this down-like country, were the White-necked Crow (*Corvus torquatus*) and its all black relative (*C. macrorhynchus*).

At Ka-chek we were entertained by the members of the American Presbyterian Mission and at once set about obtaining carriers and boats to continue our journey. The knowledge

they had of travelling conditions in the interior was of the greatest value to us, and it was due largely to their assistance that the success of our trip was due. It proved on the whole a delightful journey. The weather was cool and for the most part dry. Food, mainly pork, chickens and eggs, and hand-milled rice could be obtained in many villages, so that we were relieved of the necessity of carrying much food. A species of hairy tuber served us instead of potatoes, but green vegetables were almost unknown. We found an excellent substitute, however, in the fern *Diplazium esculentum*, the young shoots of which were just appearing and ready to be eaten. Cooked like asparagus and served with butter, they made quite a palatable dish.

From Ka-chek the first part of the journey was made by boat. We had difficulty in obtaining any, as a crowd of native soldiers had just come into the town and were seizing all the craft they could lay hands on in order to reach the coast. Three boats finally managed to evade them by hiding some miles up the river, and getting away under cover of darkness, we made a start.

By daylight the next morning the river had narrowed considerably, with low hills all round coming down to the water's edge and numerous small rapids that required skilful steering to negotiate. The country on each side was fairly well wooded, but sandy, rocky and dry everywhere ; from a collecting point of view it was not productive. At Tun-fao we changed boats. From there to Kap-hao the river is a succession of rapids, and special boats are required to ascend it. Their carrying capacity is not great, and we needed five to convey us and our kit. The scenery of this part of the country was wild and extremely beautiful, the rocky river, the swift, foaming waters and the hills all round covered with dense green jungle, all combined to make a memorable picture. At Kap-hao the remainder of our porters, who had walked across country, joined us, and picking up a guide in the village we left the river and set out for the Five Finger Mountain. We formed a party of twenty-two. In Hoi-hao also I had fortunately found a man who had lived for some years in Singapore and could speak Malay. I made him our head-man and he served also as interpreter.

The route lay by narrow paths, for the most part up and down steep hills and across innumerable streams ; they had all to be forded as bridges were non-existent. Wet feet, or more commonly wet clothes from the waist downwards, was one of the discomforts we had to put up with throughout our whole stay in the mountains ; except in camp we were never dryshod.

Two days travelling through well-wooded country brought

us to Tin-si, a small town lying on the edge of the plateau some 400 metres above sea-level. Here we left the Chinese people behind, and entered the country of the Loi, a primitive folk talking a language of their own and said to have come originally from the Lei-chao peninsula on the mainland of China. In stature they were small, the women seldom being more than 5 feet in height, but well proportioned, and had they not been so indescribably filthy, could have been quite attractive.

The country now became much wilder with fewer villages. Much of it had been denuded of forest. Jungle fires, started originally by the inhabitants to clear the land for planting, and repeated systematically at intervals, have stripped the hills and left them bare except in the ravines. Sometimes we walked for hours, an endless panorama of mountains in all directions, but most of them bare except of grass.

The Five Finger Mountain has fortunately not yet been despoiled, and still remains in all its primitive grandeur, uninhabited, and almost untouched. Evergreen forests clothe its steep sides from base to summit. At the foot we found a small village and camped near it in a dry rice-field. From there we explored the lower slopes, and discovered, at 900 metres altitude, a wood-cutter's clearing, delightfully situated on a high spur between two rocky streams. To there we moved, leaving our heavier baggage in the village below. This camp, which lay on the northern slope, formed our main collecting ground, and from it we had an excellent view of the higher parts of the mountains, three of its peaks showing up clearly when the weather permitted. Heavy mists that blotted out the landscape completely, came down every afternoon about 4 o'clock and remained until 9 or 10 the following morning ; the rest of the day was generally brilliant with sunshine. The temperature at this camp fell to about 50° F. during the night, and at midday in the sun was about 80°.

The climb to the top of the mountain was steep but not difficult. Passing through thick pine forest in dense cloud at about 1200 metres altitude, we found a clearer atmosphere above, and ascending by narrow tracks reached the top some five hours later, 1860 metres as measured by the anaeroid. The summit was clothed chiefly by a mixture of stunted pines and dwarf bamboos. As we discovered later, it was the only side of the mountain that offered an easy ascent, the other approaches being guarded by perpendicular walls of bare rock.

The journey back from the mountain was not quite the same as that taken to reach it. Instead of going to Ka-chek we retraced our steps to Tin-si and then took a direct route to Ding-an on the river. Once away from the mountains the

country was more open and fertile and villages again appeared. Game birds abounded, and for the first time we could live on our guns. Partridges (*Francolinus chinensis*), Jungle Fowl, and Green Pigeon were plentiful; the Chinese Dove (*Streptopelia chinensis*) was also common, and the birds were so fat that they were well worth shooting for the pot.

As we approached Ding-an the country became more barren, and the last day's journey, through a treeless and almost grassless country to the river, where it winds slowly over a vast sandy plain, was the most trying march of all.

From a collecting point of view the expedition was a great success. A full account of the amphibia and reptiles obtained has been published in the 'Journal of the Natural History Society of Siam', vol. vi, 1923, and descriptions of the new ferns and flowering plants found have appeared at various times in botanical journals.

The Island of Hainan lies within the Indo-Chinese subregion, and its fauna and flora, as would be expected, is related to that of the adjoining mainland. The main fact which emerges from the study of the herpetological material is that it is closely bound up with the topographical conditions already referred to. The species which inhabit the northern lowland half are those that are widely distributed over the Indo-Chinese lowlands, those that are found in the mountainous country, the area most remote from the mainland, are Chinese or Trans-Himalayan in origin, or are peculiar to the Island. The two areas are quite distinct, and must be reckoned with by all future zoogeographers.

Prof. W. E. Hoffman (Visitor) of the Lingnaan University, Canton, said that many changes had taken place in the country in the last few years, and that the interior was now much more accessible than when Dr. Smith visited it.

Mr. A. H. G. Alston asked if the natives of Hainan ate *Diplazium esculentum*. Dr. Malcolm Smith replied that he he could not say for certain, but as far as he was aware they did not.

Dr. L. Richmond Wheeler observed that the slides of Hainan reminded him of Malaya. There too the primitive tribes are found in the central, mountainous, jungle-covered areas. He enquired whether the older races of Hainan showed any affinity with those of Malaya. Though the Semang are negritos with very dark skins and frizzly hair, the Sakai races are lighter in colour with wavy hair, and their relationships with other peoples obscure.

Mr. H. W. Pugsley asked whether Dr. Malcolm Smith had observed any of the larger mammals of the Indo-Chinese region in Hainan.

Dr. Smith said that, except for one species of deer, there were no large mammals on the Island.

Miss G. Lister, Mr. R. H. Burne, Mr. Francis Druce, Mr. J. D. Macdonald and the President also spoke.

PROCEEDINGS OF THE GENERAL MEETING
29 February 1940

Mr. J. Ramsbottom, O.B.E., M.A., Dr.Sc., President, in the Chair

The Proceedings of the General Meeting held on Thursday, 15 February 1940, having been circulated, were taken as read and confirmed.

A list of names of those who had made gifts to the Library since the previous meeting was read and laid on the table.

The following Fellow signed the Obligation in the Book of the Charter and Bye-Laws and was admitted :—David Noel Jones.

A certificate of recommendation of the following candidate for Fellowship was read :—For the second time, in favour of Allan Eslick.

The President reminded the Society that the time was approaching for the nomination of Members of Council for next Session, two Foreign Members (a botanist and a zoologist) and the Linnean Medallist (a zoologist). He asked that any Fellow wishing to put forward any names should communicate them to the Assistant Secretary.

Sir Arthur W. Hill, K.C.M.G., exhibited a lantern-slide from a photograph taken by Professor C. Skottsberg when he was in the Te Anau country, South Island, New Zealand, showing what appeared to be a cloud of smoke in the distance. This proved to be drifting clouds of pollen from the dense mixed Beech forest (*Nothofagus*). The picture is reproduced in Miss L. M. Cranwell's paper 'Southern-Beech Pollens' (Rev. Auckl. Inst. Mus. II, p. 175, pl. 42 *a* : October 1939).

Mr. W. R. Price exhibited photographs taken by Mr. W. I. Croome in the Cotswold Hills, illustrating the formation of ice

on vegetation at Bagendon, near Cirencester, Glos., due to the 'Ice Storm' of January 27th, 1940, when continuous rain falling upon the freezing countryside froze drop by drop immediately it touched leaf or branch. The great weight of ice thus accumulated caused most of the side branches of the larger trees to crash to the ground, the upper parts of the more vertical branches to snap about half way up and all the telegraph poles to snap in half or be dragged out of the ground.

Major Albert Pam, O.B.E., exhibited *Pamianthe peruviana* in flower. (Described in Bot. Mag., 1923, and figured on plate 9315.)

Dr. R. W. Butcher, F.L.S., gave an account, illustrated with lantern-slides, of 'Diversity of the reaction to submergence in the Batrachian *Ranunculi*'. [Printed in full, below.]

Sir George C. Simpson, K.C.B., C.B.E., F.R.S., gave an account, illustrated with lantern-slides, of 'Possible causes of change in Climate and their limitations'. [Printed in full, p. 190.]

The President expressed the thanks of the Society to Sir George Simpson.

DIVERSITY OF THE REACTION TO SUBMERGENCE IN THE BATRACHIAN RANUNCULI.

By R. W. Butcher, Ph.D., F.L.S.

The water buttercups have attracted the attention of several systematists, e.g. Hiern (1871), Glück (1905), Felix (1910) and Pearsall (1929), and because of their polymorphism very many forms and varieties have been described. In order better to appreciate the true status of some of these, experimental plants have been grown in flower-pots of loam submerged in a well or pit, built of brick, 2×4 ft. and 2 ft. deep, where their growth and development were watched. This work is not yet complete and has lately been curtailed; but the results so far obtained seem to be of some importance in interpreting the taxonomic position of several of the described varieties.

Effect of an aërial existence.—Water buttercups growing

on drying mud at the side of a pond or stream have the following well-marked characteristics :—

Growing in water.	*Growing on mud.*
Stem elongated, flexuose.	Stem very short, stout.
Submerged leaves fine, thin elongated, dark green.	'Submerged' leaves stout, thick, short, light green.
Floating leaves, if present, well developed.	'Floating' leaves absent even on species that normally possess them.
Flowers comparatively sparse.	Flowers often very numerous, well developed and fruiting well.

The terrestrial forms have been called forma or var. *terrestris* by various authors and have even been illustrated (Moss, 1920); but my simple experiments demonstrate that such terrestrial forms are merely temporary states brought about by a change from a watery to an aërial existence.

FIGS. 1 and 2.—*Ranunculus peltatus*. (1) A young plant which was transferred as a seedling from mud to water: A, its thick aërial leaves; B, its submerged leaves. (2) A plant, which had flowered, carrying subsequently produced submerged leaves.

A young plant of *R. peltatus* was transferred in a pot from drying mud to the experimental pit and submerged. The first leaf to open out was of the typical terrestrial type, but all succeeding leaves were of the submerged type, and there were no transitional forms. After four such leaves had been formed a floating leaf expanded on the surface of the water.

Another mud plant was transferred to water and after three leaves had formed was again exposed to air. The

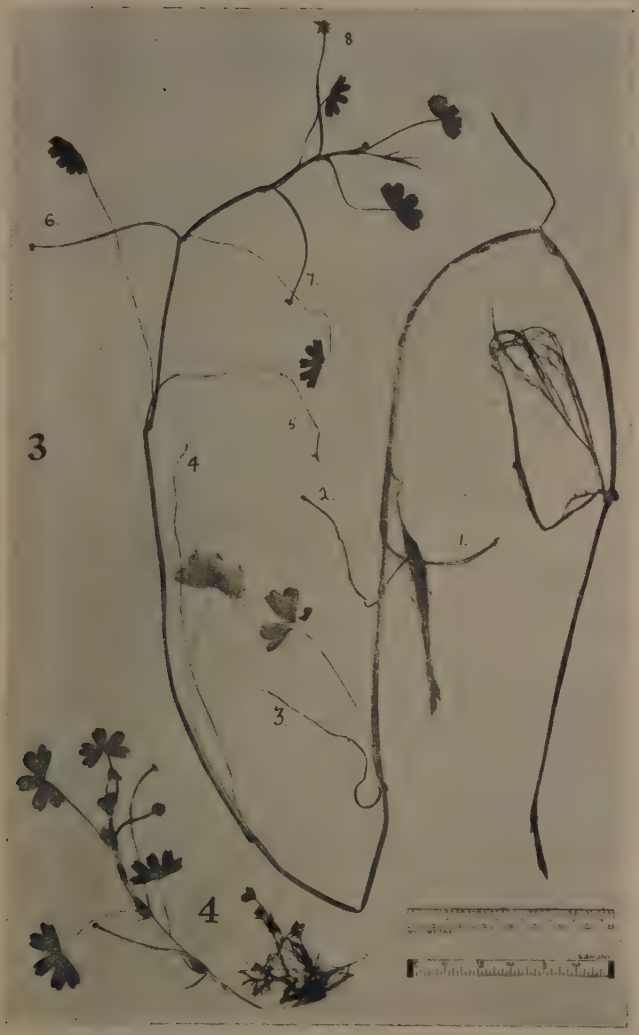
submerged leaves already formed withered, the segments of the young half-grown leaves thickened rapidly, and two more leaves of the terrestrial type developed before the mud dried up completely and the plant died.

Similar experiments were made on *R. pseudofluitans*, *R. circinatus*, *R. trichophyllus* and *R. heterophyllus*, with the same result as far as the submerged leaves were concerned. Fig. 1 is of a young plant which was transferred from mud to the pit, the short thicker leaves are lettered A, and the longer thinner leaves B. A water buttercup usually sheds its seed in July, and these apparently germinate immediately. It is inevitable at this dry season of the year that many of them germinate in the drying mud. Whether in mud or under water the cotyledons and the first leaves in the case of *R. peltatus* were observed to be identical: the cotyledons are flat, green and ovate: the first pair of leaves compound with three fine capillate segments. Thereafter the leaves arise singly and alternate, each with an increased number of segments; and the aërial and submerged leaves differ in those characteristics of slenderness and greenness which were pointed out above. Here again as soon as the young plants are submerged in the autumn they develop as normal water plants.

Effect of varying depth of water.—A young flowering plant of *R. peltatus* twelve inches long was submerged in thirty inches of water. Following this there was a rapid elongation of peduncles and petioles of the floating leaves, especially the former. The lowest peduncle, that is the one fully developed before submergence and which was flowering at the time, failed to elongate and both flower and lamina rotted away. The next petiole and peduncle elongated somewhat, but the flower bud did not reach the surface and also withered away. The third peduncle elongated even more than the second and reached the surface of the water: immediately it did so its flower opened. Each successive petiole and peduncle above this elongated just to the surface and each flower then opened. As the main stem was growing all the time toward the surface of the water, each peduncle was shorter than the one below it. This shortening continued until a minimum length of 3 cm. was attained, and at this stage the upper part of the main stem was floating on the surface of the water. This plant is shown in fig. 3 and corresponds to *R. peltatus* forma *elongatus* Hiern (1871). It is quite clear that plants so named are not varieties but mere states of the plant.

Fig. 4 represents a control plant not subjected to experimental submergence.

A similar submerging experiment was next done on *R. trichophyllus*. This plant did not elongate at all, but continued

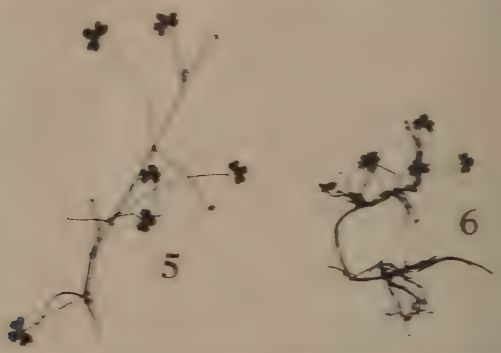


FIGS. 3 and 4.—*Ranunculus peltatus*. (3) The experimentally submerged plant described on p. 182: the pedicels are numbered. (4) A control plant not subjected to submergence.

to flower and to produce under water a few achenes on each head.

In a submerged plant of *R. Baudotii* there was a very marked elongation of the internode but not of the petiole or peduncle to the same extent as in *R. peltatus*. Some elongation did take place and the flower buds opened only on the surface and not under water.

Figs. 5 and 6 show the effect on *R. hederaceus*. There was marked elongation of petioles and main stem, but only the floating leaves were formed. *R. hederaceus* was not subjected



Figs. 5 and 6.—*Ranunculus hederaceus*. 5. An aquatic normally submerged plant. 6. A normal plant, not subjected to submergence.

to experiment, but it seems very likely from the above results that its var. *homophyllus* Tenore is simply a state produced by submergence.

It is clear that the different species experimentally examined behave differently on submergence, and it is hoped that other forms will be tested. Tentative lists of those that do and of those that do not elongate to the surface is as follows :—

Elongating.	Not elongating.
R. peltatus.	*R. trichophyllus.*
R. sphaerospermus.	*R. Drouetii.*
R. Baudotii.	*R. fluitans*
R. aquatilis.	

The shape of the floating leaf.—In all the species the shape of the floating leaf varies considerably; in none is this more marked than in *R. peltatus*, as suggested by the few outlines in fig. 7. The reason for this large variation and the systematic interrelationships are not clear. It may be recalled that Pearsall and Hanley (1927) modified the leaves of *Potamogeton perfoliatus* by growing them in various culture solutions.

and comparison of the leaves of figs. 3 and 4 shows that some modification was brought about in the leaves of the plants grown in the experimental pit. In fig. 3 some leaves are of the var. *truncatus* Koch, while others are var. *rhipidiifolius* Bast. This only serves to show how necessary it is to grow all these numerous varieties to obtain a true idea of their systematic positions.

Production of submerged and floating leaves.—The presence or absence of the floating undivided leaves of water buttercups is one of their most interesting biological characteristics. From this point of view the various species may be grouped as follows :—

1. Floating leaves never produced : *R. fluitans*, *R. trichophyllus*, *R. Drouetii*, *R. tricornutus*, *R. sphaerospermus*.

2. Floating leaves always produced when the plant is mature : *R. peltatus*, *R. tripartitus*.

3. No divided submerged leaves ever produced : *R. hederaceus*, *R. Lenormandi*.

4. Floating leaves usually produced, but at times a plant may mature without them : *R. aquatilis* (incl. *R. heterophyllus*, *R. radians* and *R. Godronii*) and *R. Baudotii*.

Species with floating leaves and varieties without them, or, vice versa, species without floating leaves and varieties with them, may often be seen in the systematic lots tossed together. **Examples of such are :—**

R. heterophyllus and var. *submersus* without floating leaves.
R. Baudotii and var. *marinus* without them.
R. trichophyllus and var. *radians* with them.
R. fluitans and var. *heterophyllus* with them.

R. fluitans, *R. pseudofluitans* and *R. trichophyllus* have been grown continuously in the pit for three years where they never produced a vestige of a floating leaf, while *R. radians* and *R. heterophyllus* always produced them. On the other hand, a plant of *R. Baudotii* var. *marinus* produced floating leaves a week after it was put in the pit. In this connection it should also be pointed out that the environment of the plant does not influence this characteristic to any marked degree. Plants growing in running water often have floating leaves, while there are several still-water species that never possess them.

The growth-history of an individual plant of *R. peltatus* throws a little light on the conditions of development of the leaves. From October, when it was first gathered, until March, a ruff of capillate leaves remained dormant in the pot. During March, elongation of the stem to the surface took place : the first floating leaf was produced on April 12th, and flower on April 22nd. It continued to produce floating

leaves and flowers until the middle of June, when, at the apex of both main stem and branches, capillate leaves were again produced. Elongation of the stems then almost ceased. After producing a rosette of 3–6 capillate leaves, adventitious roots grew from its base, the main stem rotted away and the small rosettes floated about independently. This stage of growth is shown in fig. 2.

These observations, together with the fact that terrestrial forms produce floating leaves, albeit rarely, support the contention that floating leaves are developed when growth

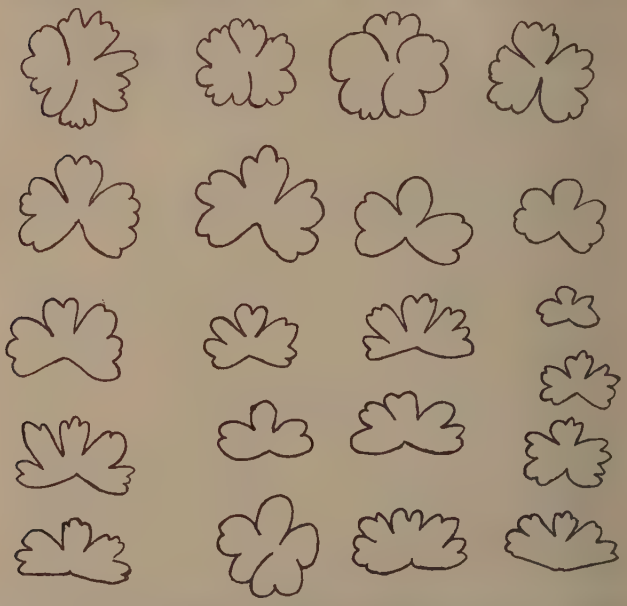


Fig. 7.—Floating leaves of *Ranunculus peltatus*, illustrating variation in outline: mostly from specimens in the Druce Herbarium.

conditions are favourable and not when they are poor. This remark does not apply to those species that never produce floating leaves.

Change in environment.—The only important change made in the environment of the plants was to transfer them from running to still water. The reverse was attempted but the plants did not grow in the river. There were also no obvious differences between plants grown in hard water and plants grown in rain-water. *R. Baudotii* did, however, grow quite well for three years in rain-water.

Some of the running-water plants changed remarkably in the pit; but some retained their characters. *R. fluitans* scarcely altered at all. The leaves remained elongated and the stem grew nearly three feet long, zig-zagging about the pit, but never rising direct to the surface. Flowering was, however, sparse. The plant of *R. pseudofluitans* was only a little less robust in the pit than those in the nearby river Itchen. A plant from a New Forest stream, however, became

FIGS. 8–12.—Winter conditions of: (8) *R. Baudotii*; (9) *R. pseudofluitans*; (10) *R. sphaerospermus*; (11) *R. peltatus*; and (12) *R. peltatus* var. *penicillatus*.

shortened in stem; the leaves became less elongated; and after two years it was only slightly different from *R. peltatus*. Another remarkable plant from near Wimborne, Dorset, which had a thick stem, very large and multi-segmented submerged leaves, immediately lost this robustness when grown in the pit.

The winter states.—Many of the water buttercups pass the winter as plants with submerged leaves only. In most of the running-water forms, the winter and summer leaves are alike, but in the pond forms they are remarkably different, and some of these are shown in figs. 8–12. Such submerged winter leaves are usually flaccid and collapse into a tuft when taken out of the water. This represents a remarkable change in those species such as *R. trichophyllus*, *R. peltatus* and *R. sphaerospermus* which in summer have stiff divaricate leaves, and raises questions as to the value of this character ('leaves rigid or collapsing'), which is used to distinguish certain species. The greatest change seems to occur in *R. circinatus*. The small stiff disciform leaves of the summer were replaced in winter by leaves with semi-divergent segments disposed in the form of a cone. This form is illustrated by Glück (1905) and named *R. circinatus* f. *capillaceus*. In shape of leaf it corresponds to a plant that grows, totally submerged, in Rescobie Loch usually called *R. trichophyllus* var. *subaquaneus* Wallr.; but Pearsall (1929) refers it to *R. circinatus* var., and from the evidence of seasonal change of leaf-shape, among other things, this view would appear to be the correct one.

Conclusion.—These cultivation experiments will be continued when opportunity offers, and it is hoped that they will elucidate further the causes of variation in these interesting plants. Even these preliminary notes indicate certain amendments needed in the classification of the group, as follows:—

(1) Plants exposed to the air form transitional states that are hardly worthy of mention in any taxonomic system.

(2) There are probably too many forms given specific rank; but to group all under one species *R. aquatilis* is equally erroneous.

(3) Many so-called forms and varieties are simply states of the plant that change with changing environment:

R. peltatus f. *truncatus* Koch, f. *quinquelobus* Koch, and f. *rhipiphyllus* Bast. are leaf forms;
R. peltatus var. *elongatus* Hiern is a deep water state;
R. Baudotii var. *marinus* is a young state.

(4) Although immature forms may lack the normal floating leaves produced by healthy plants it is not correct to assign to them a higher status than 'forma'. Also it seems unlikely that species which do not produce floating leaves under optimum conditions will produce them under other circumstances. The classification of *R. trichophyllus* var. *radians* and var. *Godroni* would be more correct as *R. aquatilis* (=*heterophyllus*) var. *radians* and var. *Godroni*.

Note.—The sources of the plants grown in the pits are as follows. Only one strain of each species mentioned was used :—

R. fluitans Lam. Bristol Avon, Chippenham.
R. circinatus Sibth. Lewes levels, Sussex.
R. trichophyllus Chaix. Ludgershall, Wilts.
R. Drouetii F. Schultz. Southwick, Hampshire.
R. peltatus Schrank. Cadnam, Hampshire.
R. peltatus var. *penicellatus* Dum. Highland Water, Hampshire.
R. pseudofluitans Baker & Foggitt. R. Itchen, Alresford, Hampshire.
R. sphaerospermus Boiss. Canal, Greywell, Hampshire.
R. Baudotii Godr. Sandwich Golf Links, Kent.
R. lutarius Bouvet. Brockenhurst, Hampshire.

These plants are the same as those illustrated in Butcher & Strudwick (1930).

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Discussion.—

Mr. A. J. Wilmott and the President said they hoped that this experimental work would be continued : and Mr. J. S. L. Gilmour suggested the possibility of finding evidence of genotypically different forms correlated with different habitat conditions.

POSSIBLE CAUSES OF CHANGE IN CLIMATE AND THEIR LIMITATIONS.

By Sir George C. Simpson, K.C.B., F.R.S.,
President of the Royal Meteorological Society.

The meteorologist has no first hand knowledge of changes of climate, and when he is asked to explain a change of climate he naturally asks for a clear statement of the change of climate he is to explain. The only certain knowledge there is of changes of climate is provided by the geologist. The evidence which geology can give is very fragmentary, and in the best of cases is confined to the existing land surfaces which cover only a fraction of the earth's surface. The element of time is also of importance, a geological period is a very long time, and evidence of climatic changes in different parts of the world, although clearly belonging to one geological period, may not have been simultaneous. This is particularly true of the earlier geological periods. The evidence of climate in these early periods, as I shall show later, is not consistent with physical possibilites; for example, we are told that during the Permo-Carboniferous Period the southern hemisphere was largely glaciated even up to the equator while the northern hemisphere was not only not glaciated, but conditions, which we now associate with the subtropics, extended up to and beyond the Arctic Circle. Such a conjunction of climates is quite impossible from a meteorological point of view.

Further, we are told that during the Eocene Period there was a uniform, warm, damp and calm climate from Pole to Pole without any sign of the climatic belts which we now have. If this is true the meteorologist cannot explain it, for so long as the earth is a sphere and the sun is the source of radiation there must be climatic belts with an appreciable difference of temperature between the equator and the poles.

It was to meet these apparent inconsistencies in the geological record that Wegener, a meteorologist, put forward his theory of the drift of the continents and the shift of the poles. That took the problem out of the hands of the meteorologists and left it in the hands of the geologists and there it must remain for the present.

There are, however, other geological evidences of changes of climate in times so recent that there can have been no major geographical changes. The Pleistocene Period has afforded evidence of great and repeated changes of climate, of glaciation extending from the North Pole to latitude 40° N., of pluvial periods in many parts of the world with many times the present rainfall, at least locally, and of conditions in Europe when the presence of *Corbicula fluminalis* in the rivers of Great Britain, and Mediterranean fauna in the sea around north-west Europe

clearly show a rise of temperature of between 5° and 10° C. The correlation of even these great climatic changes in such relatively recent times is far from being worked out, and the geologist cannot give to the meteorologist a clear picture of the climate of the world at any one epoch. The meteorologist has, therefore, first to reconstruct his own picture of the climate, which the geologist seldom accepts, and then to endeavour to explain the picture he has drawn.

For these reasons ice ages and pluvial periods will bulk largely in this attempt to describe some possible causes of climatic change and their limitations; for if only we can explain a single glacial epoch and find its relation to a pluvial period I feel sure we shall have the key to the whole climatic problem in our hands.

Before I proceed to the main subject of my lecture I would like to say a few words about the difficulty the meteorologist has in discussing this problem.

Meteorology is a branch of physics, and physics makes use of two powerful tools: experiment and mathematics. The first of these tools is denied to the meteorologist and the second does not prove of much use to him in climatological problems. The factors involved in determining the climate of a place are so many and so interrelated that they cannot be expressed in mathematical form except with so many simplifying assumptions that the result is seldom quantitative even if it is qualitative. As we cannot calculate the mean temperature of a place, much less the rainfall and the wind, we cannot say what will be the magnitude of the change in climate for a given change in any of the factors controlling it. Without numerical values our deductions are only opinions and open to the criticism of any one who has formed other opinions from the same facts.

Several mathematicians have, however, made brave attempts to calculate climate, and the most successful is probably Milankovitch in his monograph 'Mathematische Klimalehre und Astronomische Theorie des Klimaschwankungen' (1930), about which I shall have a lot to say later on. In this attempt Milankovitch has to make many assumptions which we know are wrong and has to neglect many things which we know are important. In consequence his work has the failings which I have just mentioned, and I shall have to criticize his numerical values; nevertheless, his work is valuable, and his mathematical methods are instructive.

As we are unable to solve our problems by theoretical calculations we are thrown back upon empirical methods. That is, we must examine the present climate and try to find the causes of the variations from place to place by studying the varying amounts of radiation received and the geographical

conditions. We shall confine our attention chiefly to temperature and rainfall, as these are the two climatic elements which are best represented in the geological record.

One of the most favourite explanations of change of climate is a change in the distribution of land and water. More than one theory of the cause of the Pleistocene Ice Age has been based on a change in the amount of land in high northern latitudes, aided, it is true, in some cases by an elevation of the land surface. We will therefore take this geographical theory of the cause of the change of climate as the first theory for examination. We will first study the effect which the present distribution of land and water has on the climate.

The empirical method is well suited for this purpose, for we can compare the climate of places similarly situated as regards the solar radiation they receive, but differently situated as regards the amount of land and sea around them.

The Geographical Theory.
(Change in Land and Water.)

A circle of latitude in the northern hemisphere receives exactly the same amount of solar radiation in the course of a year as the corresponding latitude in the southern hemisphere. The amount of land along a specified circle of latitude is, however, often quite different in the two hemispheres. Hence, if we compare the temperature of the same latitude in the northern and southern hemispheres we shall be able to see what effect the amount of land has on the temperature. We must for this purpose use the mean annual temperature, for the radiation is the same in the two hemispheres only when we consider the year as a whole. The data are contained in Table I.

In column 8 we have the mean annual temperature of the circles of latitude in the northern hemisphere and in Column 9 corresponding values for the southern hemisphere, and Column 10 gives the difference. We see that in all latitudes the northern hemisphere is the warmer; but the mean difference (taking account of areas) is only 2° C. Considering that there is twice as much land in the northern as in the southern hemisphere (34 and 19 per cent. respectively, see Columns 11 and 12), we see at once that the effect of the land is only small, if the whole of the difference can be ascribed to that cause. This conclusion is reinforced when we examine the individual latitudes. No circle of latitude in the northern hemisphere is more than 3° C. warmer than the corresponding latitude in the southern hemisphere (omitting latitudes 80° S. and 90° S. where the conditions are abnormal owing to the great Antarctic plateau enclosed within latitude 80° S.), yet the

TABLE I.

Mean temperature of the latitude circles, °C.

Latitude.	North.			South.			Year.			Percentage of Land.	
	July.	Jan.	Difference.	Jan.	July.	Difference.	North.	South.	Difference.	North.	South.
0.....	25·6	26·4	−0·8	26·4	25·6	+0·8	26·2	26·2	—	22	22
10.....	26·9	25·8	+1·1	26·3	23·9	+2·4	26·7	25·3	+1·4	24	20
20.....	28·0	21·8	+6·2	25·4	20·0	+5·4	25·3	22·9	+2·4	32	24
30.....	27·3	14·5	+12·8	21·9	14·7	+7·2	20·4	18·4	+2·0	43	20
40.....	24·0	5·0	+19·0	15·6	9·0	+6·6	14·1	11·9	+2·2	45	4
50.....	18·1	−7·1	+25·2	8·3	3·0	+5·3	5·8	5·5	+0·3	58	2
60.....	14·1	−16·1	+30·2	1·2	−10·3	+11·5	−1·1	−4·1	+3·0	61	0
70.....	7·3	−26·3	+33·6	−1·3	−23·9	+22·6	−10·7	−13·3	+2·6	53	71
80.....	2·0	−32·2	+34·2	−7·4	−36·3	+28·9	−18·1	−24·7	+6·6	20	100
90.....	−1·0	−41	+42	−11	−42	+31	−22·7	−30	+7	—	—
Hemisphere ...	22·4	8·1	+14·3	17·0	9·7	+7·3	15·2	13·3	+1·9	39	19
Earth	...	...	...	...	...	...	14·2		...	29	

amount of land along some of the northern circles of latitude is many times greater than along the corresponding southern latitudes. Combining the three latitudes 40°, 50° and 60°, which represent a quarter of the earth's surface, and where the temperature data are well determined, the mean temperature of this zone in the northern hemisphere is only 1·8° C. higher than that of the corresponding zone in the southern hemisphere, yet the northern zone contains 55 per cent. of land and the southern zone only 2 per cent.

In Table I we see the mean temperature of the zones of latitude decreasing from the equator to the poles, and the rate of decrease being to all intents and purposes the same in both hemispheres, quite independently of the different amounts of water and land and of its distribution. This shows what little part the surface conditions play in determining the general distribution of temperature at sea-level when the world is considered as a whole. The general temperature distribution is determined by two main factors: (*a*) certain physical qualities of the atmosphere, and (*b*) the spherical shape of the earth which determines the distribution of solar radiation. Neither of these two factors can have changed appreciably in the long history of the world, at least since the geological record of climate commenced, and therefore there must always have been a decrease of the temperature from the equator to the poles, and the mean temperature of corresponding latitudes must have been the same in both hemispheres. This necessitates similar climatic conditions in the two hemispheres at all times and therefore a glaciated southern hemisphere and a warm northern hemisphere, as is suggested was the case in the Permo-Carboniferous Period, is entirely impossible; as is also a glaciated equator and a subtropical Arctic which would involve a reversal of the essential decrease of temperature from the equator to the poles. The uniform temperature over the whole earth, which is said to have existed in the Eocene Period, is equally impossible.

So far we have dealt with the mean temperature of a whole zone; when we come to examine the difference of temperature at different localities within the same zone the matter is not quite so simple.

Within 40° of the equator, i.e., for considerably more than half (64 per cent.) of the earth's surface, the continents are warmer than the oceans; while for the remainder of the surface the continents are colder than the oceans. The difference can reach appreciable amounts; for example, the North Atlantic Ocean in latitude 70° N. in the neighbourhood of the coast of Norway is, on the average of the year, more than 12° C. warmer than its latitude warrants; but it is compensated by cold regions over the continents of Asia and

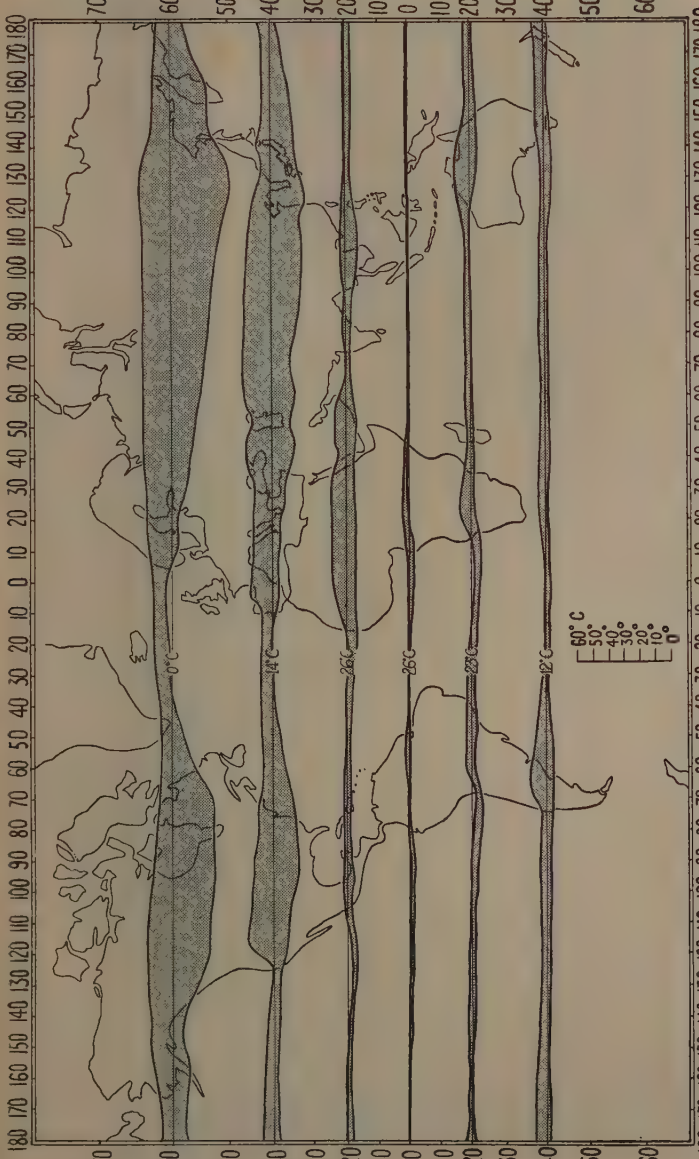

FIG. 1.—Annual range of temperature.

North America, so that the mean temperature of the latitude as a whole falls into its right position in the normal decrease of temperature from the equator to the pole.

This compensation of every region of abnormal temperature, whether brought about by ocean currents or prevailing winds, by one or more regions of opposite abnormality is an important corollary of the empirical law that the mean temperature of the latitude is independent of the surface conditions and must be taken into account in discussing possible changes of climate due to changes in the distribution of land and water.

It is when we examine the temperatures of the summer and winter months that we see the effect of the surface at its maximum. Two places may have the same mean annual temperature, but very different summer and winter temperatures. The difference in temperature between the warmest and coldest month is called the annual range of temperature, and is highly dependent on the nature of the surface : whether water, land or ice. I have attempted to illustrate this in a novel way in fig. 1. This is a map of the world on Mercator projection. I have drawn in lines representing the equator, latitude 20° and 40° north and south and 60° north. Using these lines to represent the mean annual temperature of the whole latitude, I have marked off the mean temperature of January and July as representing the warmest and coldest month of the year. The same scale of temperature has been used for all the latitudes, and is shown at the bottom of the chart.

Examining the curves for the equator we see, as we should expect, little or no difference between the warmest and the coldest months. Turning to one of the higher latitudes, say 40° N., we see that over the land the annual range of temperature is large, being as much as 30° C. over North America and nearly 40° C. over Asia ; on the other hand, the annual range falls to as little as 6° C. over the east of the Atlantic. In the southern hemisphere latitude 40° runs almost entirely over the ocean and the range is very small, only exceeding 6° C. in the neighbourhood of the land. The effect of the land in increasing the annual range of temperature is most clearly seen in the curves for latitude 60° N. : over the North Atlantic the range is locally as small as 8° C. ; but over Asia it rises to a maximum of 58° C.

The temperature of the warmest and coldest months has a more profound effect on the climate of a place than the mean temperature. Temperature, however, is not well represented in the geological record except as the factor affecting glaciation. I will therefore confine my remarks to this aspect of the annual range of temperature.

It is well known that summer temperatures are the main

deciding factor for glaciation. Generally speaking the temperature of the warmest month is above 5° C. in non-glaciated regions and below in glaciated regions; the temperature of the coldest month is of little importance.

The great contrast between the conditions on latitude 70° in the northern and southern hemispheres is very instructive. The mean annual temperature of the two circles is not very different, namely −10·7° C. and −13·3° C. respectively, both well below 0° C. Yet 70° S. is completely glaciated right down to sea-level; while there is no permanent ice at sea-level anywhere on latitude 70° N. The reason is not difficult to find. On the equatorial side of latitude 70° N. there are the great continents of Asia, Europe and North America with their high summer temperatures. The consequence is that the mean temperature of the warmest month along latitude 70° N. is 7·3° C., i.e. a temperature too high for glaciation. On the other hand, on the equatorial side of latitude 70° S. we have the Antarctic Ocean with its very low summer temperatures; in consequence, the midsummer temperature at latitude 70° S. is −1·3° C. and everywhere is glaciated. The difference in the conditions in these two latitudes is not the result of the relative amount of land and water (there is 71 per cent. land along latitude 70° S. compared with 53 per cent. along 70° N.), but to the distribution of the land and water. We therefore see that very large differences of glaciation are produced by differences in the distribution of the land, and we shall see shortly that the same applies to deserts in lower latitudes.

In this discussion of the temperature I have not introduced the effect of the height of the land above sea-level; what has been said refers only to sea-level. The effect of height is, however, simple. For individual mountains and mountain ranges the temperature is approximately that of sea-level reduced at the rate of about 3° F. per thousand feet. The temperatures on plateaux are somewhat more complicated. The effect of mountains is purely local and can have little effect on altering the mean temperature when reduced to sea-level. As a means of radically altering the climatic conditions of a given circle of latitude, beyond the immediate local effect, changes in height are unimportant.

When we come to study the present distribution of rainfall we find that it is much more complicated than that of temperature. The distribution can best be studied by the aid of a map of the world showing the mean annual rainfall, such as that prepared by W. Meinardus and published in the fifth edition of Hann-Suring's ' Lehrbuch der Meteorologie '.

The distribution of rainfall depends on three main factors:

(*a*) A latitude effect.

(*b*) An orographic effect (irregularities in the height of the surface).

(*c*) The direction of the prevailing winds.

The latitude effect leads to three main zones of rainfall in each hemisphere.

(1) An equatorial zone of heavy rain (0°–10°).

(2) A sub-tropical zone of low rainfall in which the main deserts occur (10°–30°).

(3) A zone of medium rainfall in which the rainfall is mainly associated with cyclonic disturbances (30°–90°). The maximum rainfall in this zone occurs at about latitude 45° and then falls off to polar regions, where it becomes very small.

The orographic effect is mainly associated with the great mountain ranges. When a range of mountains runs athwart the prevailing wind there is heavy rain on the windward side and a rain shadow on the leeward side, often extending for long distances away from the mountain range. Examples are the Rocky Mountains of North America, the Andes of South America and the Western Ghats of India, each of which has heavy rain on the windward side and an area of scanty rain on the lee side.

The effect of the prevailing winds depends chiefly on the origin of the air. If this is a warm damp region heavy precipitation occurs, while if it comes from a cold or dry region little rain falls. The west coast of Europe is relatively wet because the prevailing winds are from the south-west, while the coast of North America in the same latitude is dry because the winds there are mainly from the north and west, in the former case cold and in the latter dry. The effect of the wind, however, is seen at its maximum in the great monsoon areas, such as India, south-east China and northern Australia.

These three effects, mutually independent, may work in the same or in opposite directions. In consequence, the distribution of rainfall is very irregular, and extremes of rainfall may be found in all three zones. In the north equatorial zone with an average annual rainfall of 170 cm., and with many places where the rainfall exceeds 300 cm. in the year, there is an appreciable area in the neighbourhood of Cape Guardafui in Somaliland with an annual rainfall of less than 25 cm. Similarly, in the desert zone 15° to 35° N. we have both the North African deserts with practically no rainfall at all and the Indian monsoon area where the rainfall rises locally to 1161 cm. in the year—one of the wettest spots on the earth. Even in the temperate zone we have rainfall of well over 300 cm. a year along the west side of the Andes in Chile between latitudes 40° and 50° S. and less than 25 cm.

in its rain shadow in Patagonia. With such tremendous variations of rainfall in each zone, all caused by the relative distribution of land and sea, one would not be surprised if the rainfall in the northern hemisphere with its 39 per cent. of land were different from that in the southern hemisphere where the land is only 19 per cent., i.e. half as much as in the northern hemisphere. In fact, the total rainfall of the two hemispheres is the same to 1 per cent. The rainfall in the corresponding zones in the two hemispheres, in spite of the entirely different distribution of land and sea in each, is remarkably similar, as will be seen from Table II. Even in the zone

TABLE II.

Average rainfall in zones.

Zone.	Rainfall in centimetres.		Area of Land percentage.	
Lat.	N.	S.	N.	S.
0–15.....	170	138	23	23
15–35.....	84	91	36	22
35–60.....	86	111	52	3
60–90.....	34	28	50	40
Hemisphere	99·7	100·7	39	19

35°–60°, which is half land in the northern hemisphere and practically all sea in the southern hemisphere, the mean rainfall of the two only differs by 25 per cent. of the mean total. One can only draw from this the conclusion that, while the distribution of land and sea can cause very large variations in the local rainfall, the rainfall of the world as a whole, like the temperature, is mainly controlled by factors other than the distribution of land and sea.

From this rapid review of the existing climates and their relationship to the present distribution of land and water two main conclusions stand out :—

(*a*) The temperature and rainfall when considered as the average for a zone and a year are the same in the two hemispheres for corresponding latitudes, irrespective of the amount and distribution of land and water ; from this we may conclude that it is the shape of the earth and the physical properties of the atmosphere which determine the main features of the climate of the earth as a whole.

(*b*) The distribution of land and water mainly affect the annual variation of temperature and the amount of rainfall; in consequence large variations of climate are possible within a zone, and glaciation and desert formation are very largely the effect of the local distribution of land and water.

Applying these results to our main purpose, namely, to find a cause for climatic change, it would appear that we have in the distribution of land and water a possible cause of climatic change. But examining the geological record we see that this has not been the cause of the violent changes in climate recorded during the Pleistocene Period. During that period there were climatic changes which might have been brought about by a redistribution of land and water; but the climatic conditions oscillated between very large limits and the same oscillations were apparently repeated several times. It is incredible that each of these climatic oscillations was brought about by an oscillation in the distribution of land and water, and there is no geological evidence of such geographical changes. We must therefore accept the conclusion that while alterations in land and water may cause important changes in the climate such alterations were not the cause of the large climatic changes which occurred during the Pleistocene Period. There are, therefore, other causes of climatic change than redistribution of land and water.

The Astronomical Theory.

(Changes in the Earth's Orbit.)

For over a hundred years astronomers and some geologists have been impressed by the possibility of appreciable variation in climate being due to the changing aspect which the earth presents to the sun as the elements of the earth's orbit go through their periodic changes.

John Herschel was, I believe, the first to raise the question, and he was followed by such outstanding authorities as Arago, von Humboldt, Robert Ball, George Darwin, and James Croll. I do not propose to follow all these great men in the long and unsatisfactory controversy which lasted throughout the nineteenth century. They were handicapped, just as we are, by their inability to find a method of calculating the effect on the temperature of the earth's atmosphere of a change in the amount of radiation received. The controversy came to an end because the geologist was unable to find the long succession of periodic changes of climate which the theory demands. The geologists recognize three or four ice ages at very long intervals, even as geological time goes, while the astronomical theory would give several ice ages in a million years.

Little was heard of Croll's Theory in the present century until in 1926 a modified astronomical theory of change of climate was put forward by Köppen and Wegener as part of their theory of climate change due to movement of the continents. The history of this revival is important if we are to judge the success of the theory in providing the explanation of the climatic changes determined by recent geological and archaeological work.

Wegener's theory of the drift of the continents and the so-called shift of the pole is well known. This theory was developed mainly to explain climatic changes which Wegener, as a meteorologist, knew were not possible if the continents had always maintained their present position relative to the polar axis. The meteorological investigation was taken up by Wegener in collaboration with the well-known meteorologist Köppen, and, after tracing the movement of the poles through the early geological periods and so explaining in broad outline the climate of those periods, they found that towards the end of the Pliocene Period the North Pole was approaching Greenland from the west almost along the northern coast of North America. At the beginning of the Pleistocene the Pole reached, according to their computations, the west coast of Greenland in the neighbourhood of where latitude 70° N. now crosses the coast. From this point the movement was slowed down, and the Pole remained in the centre of Greenland until the end of the Würm glaciation, when it made a rapid movement to its present position. Thus throughout the Pleistocene Ice Age the North Pole was between 5° and 7° nearer to north-west Europe than it is at present, and it was in this fact that Köppen and Wegener saw the primary cause of the Pleistocene Ice Age.

They were, however, in a difficulty, for the geological evidence had by that time become clear that the Pleistocene Ice Age did not consist of one long period of low temperature, but consisted of a series of glacial and interglacial epochs representing changes of climate equivalent to latitude changes of between 5° and 10°, and even they were not prepared to ascribe these to wanderings of the Pole (Köppen and Wegener, 1924).

About this time, 1920, Prof. Milankovitch of the University of Belgrade had published a book entitled 'Théorie mathématique des phénomènes thermiques produits par la radiation solaire', in which he had taken up again the old problem of the changes in the solar radiation received by the earth due to the changes in the elements of the earth's orbit. Köppen and Wegener were impressed with the large changes in summer and winter radiation when expressed in terms of equivalent latitude changes. Köppen and Wegener gave

reasons for considering that the changes in the winter radiation were unimportant when questions of glaciation are under consideration, while the summer radiation is all important. Fixing their attention then on the value of the mean radiation received during the summer half year, they found variations in radiation for latitude 65° N. which were equivalent to changes of latitude of over ten degrees.

I reproduce here (fig. 2) the curve of variations of radiation for the summer half-year for latitude 65° N. as finally published by Milankovitch, which is slightly different from the curve used by Köppen and Wegener. Here the variations of radiation are expressed in equivalent latitudes; for example, in the summer 10,000 years ago the radiation received in latitude 65° N. was the same as is received in the summer at the present time in latitude 60° N.; therefore 60° N. is the equivalent latitude for the summer radiation in 65° N. 10,000 years ago.

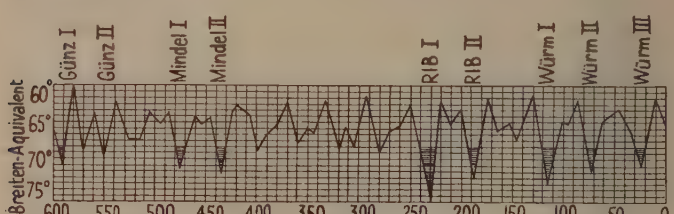

Fig. 2.—Summer radiation for 65° N. in latitude equivalents. Calculated by M. Milankovitch.

Köppen and Wegener noticed that in their curve there were eight periods in each of which the departure was more than 3°, that is the equivalent latitude exceeded 68° N. (in their curve the departure at year—25,000 did not quite reach latitude 68° N. so that it was not counted) and that these eight periods naturally fell into four pairs.

This appeared to them very significant, and they wrote: ' we recognize in the zigzag line of the curve four pairs of groups of cold summers each embracing many thousands of years, these pairs being centred about 90,000, 210,000, 450,000 and 570,000 years before the present era correspond approximately with the middle of the Würm, Riss, Mindel and Günz glacial periods according to the estimates of Penck and Brückner for the Alpine region. The probability of such a connexion is considerably enhanced by the large interval between the second and third pairs which corresponds to the " great interglacial " ' (Köppen and Wegener, 1924, p. 217).

Thus by combining the four pairs of large departures each into a glacial epoch Köppen and Wegener recognize in the radiation curve a correspondence with the well-known curve of the advance of the snow line in the Alps published by Penck and Brückner thirty years ago (Penck and Brückner, 1901–9).

Köppen and Wegener, however, make it quite clear in their book that the variations in the solar radiation do not cause the Ice Age ; but only the subdivision of the Ice Age into glacial and interglacial epochs. The cause of the Ice Age, according to them, was the approach of the Pole towards the middle of Greenland, and the Ice Age came to an end when the Pole moved on to its present position (Köppen and Wegener, 1924, pp. 224–32).

The possibility of dating the varying episodes of the Pleistocene Ice Age by correlating them with the radiation curve appealed to a number of workers in this branch of science. Correlations with the radiation curve were found everywhere : the deposits assigned to each of the first three glaciations were found to be double and three maxima were recognized in the deposits of the Würm glaciation, and evidence of severe climates not amounting to glacial epochs were found for some of the minor departures on the radiation curve. In fact, every departure towards cold summers and some towards warm summers shown by the radiation curve was found to be represented in the glacial and other deposits at one or more sites. The following quotation illustrates this :

> ' The correspondence between the geological facts and the variations of the summer radiation is not confined to a general similarity ; it is the details (Einselheiten) which testify so convincingly in support of the correlation between the astronomical curve and the stratigraphic sequence ... Further, even the relative intensities of the glaciations find their explanation in the radiation curve ' (F. E. Zeuner, 1938).

It is clear from the last sentence of this quotation that Köppen and Wegener have been completely forgotten, and all the variations of the climate are now ascribed to the changes in the solar radiation—there is no room for any movement of the Pole.

We must now look a little closer into the basis of this claim that the history of the climate during the Pleistocene can be explained and dated by astronomical calculations.

There are three elements of the earth's orbit which undergo periodic changes :

(1) e, the eccentricity of the orbit.
(2) Π, the longitude of the equinox.
(3) ϵ, the inclination of the earth's axis to the ecliptic.

The values which these three elements have at any time determine the amount of radiation received by each point on the earth's surface (neglecting the atmosphere) while the earth moves over a specified portion of its orbit.

For our purpose the following facts are important.

(*a*) At all times, no matter what may be the values of each or all of the elements of the orbit, the total amount of radiation received by the northern hemisphere in a year is constant and exactly the same as that received by the southern hemisphere. Thus variations in the elements do not affect the total radiation received either by the world as a whole or by the two hemispheres.

(*b*) Variations in the eccentricity of the orbit and the longitude of the equinoxes do not alter in any way the total radiation received by a point of the earth's surface in the course of a year, but they do alter the amounts received in the summer and the winter *. The excess radiation received in the summer is balanced by an equal defect in the winter and vice versa.

(*c*) Variations in the inclination of the earth's axis cause an increase or decrease of the radiation received by places between latitude 43° and the pole, and opposite changes in latitudes between 43° and the equator. The changes are of equal amount and of the same sign in both hemispheres.

The changes in radiation have been calculated by Milankovitch for specified years at intervals of 5,000 years right back to 600,000 years before 1800 A.D. Values for latitudes 25, 35, 45, 55, 65 and 75 degrees in each hemisphere are published in his work mentioned above (Milankovitch, 1930, Table 15). Fig. 2 gives the values for the summer half year in latitude 65° N. expressed as equivalent latitudes.

Milankovitch has also given a formula for calculating from the values of the radiation the corresponding changes in temperature. Using this formula, I have calculated the change in temperature of the warmest and coldest months and of the year as a whole at five special epochs and give the values in the upper half of Table III. I have chosen the

* Summer and winter are used here and throughout this portion of the lecture in a specialized sense defined by Milankovitch. The year is not divided into summer and winter exactly at the equinoxes which would divide the year into unequal parts; but the year is divided into two equal halves in such a way that every day in the summer half receives more radiation than any day in the winter half.

TABLE III.

Temperature differences (present—past).

Latitude. ° N.	Günz I. Year 590·3.			Mindel II. Year 433·6.			Riss I. Year 232·4.			Würm I. Year 116·1.			Climatic Optimum. Year 11·1.		
	July. ° C.	Jan. ° C.	Year. ° C.	July. ° C.	Jan. ° C.	Year. ° C.	July. ° C.	Jan. ° C.	Year. ° C.	July. ° C.	Jan. ° C.	Year. ° C.	July. ° C.	Jan. ° C.	Year. ° C.
Milankovitch's Method.															
25	−4·5	+4·9	+0·2	−2·1	+2·8	+0·3	−4·2	+4·9	+0·4	−4·6	+5·2	+0·3	+7·4	−7·8	−0·2
35	−4·6	+4·8	+0·1	−2·7	+3·0	+0·2	−4·6	+5·0	+0·2	−4·9	+5·2	+0·2	+7·1	−7·3	−0·1
45	−4·4	+4·4	0·0	−3·3	+3·2	0·0	−5·0	+5·0	0·0	−5·1	+5·1	0·0	+6·6	−6·6	0·0
55	−4·3	+3·9	−0·2	−3·8	+3·1	−0·4	−5·4	+4·6	−0·4	−5·2	+4·5	−0·3	+6·0	−5·6	+0·2
65	−4·1	+3·0	−0·5	−4·5	+2·6	−1·0	−6·0	+3·8	−1·1	−5·4	+3·6	−0·9	+5·3	−4·3	+0·5
75	−4·0	+1·9	−1·0	−5·4	+1·7	−1·9	−6·7	+2·4	−2·1	−5·7	+2·3	−1·7	+4·6	−2·6	+1·0
Revised Method.															
25	−0·8	+0·9	+0·1	−0·4	+0·6	+0·1	−0·8	+1·0	+0·1	−0·8	+1·0	+0·1	+1·4	−1·5	−0·1
35	−1·0	+1·1	+0·0	−0·6	+0·7	+0·1	−1·0	+1·2	+0·0	−1·1	+1·2	+0·1	+1·6	−1·6	−0·0
45	−1·1	+1·1	0·0	−0·8	+0·8	0·0	−1·2	+1·2	0·0	−1·2	+1·2	0·0	+1·6	−1·6	0·0
55	−1·1	+1·0	−0·1	−1·0	+0·8	−0·1	−1·5	+1·2	−0·2	−1·4	+1·1	−0·1	+1·6	−1·4	+0·1
65	−1·2	+0·7	−0·2	−1·4	+0·6	−0·4	−1·8	+0·9	−0·5	−1·6	+0·8	−0·4	+1·5	−1·1	+0·2
75	−1·2	+0·3	−0·4	−1·7	+0·2	−0·8	−2·1	+0·3	−0·9	−1·8	+0·4	−0·7	+1·4	−0·6	+0·4

temperature of the warmest and coldest month rather than the mean summer and winter temperatures, as the former can be compared with the mean temperature of July and January at present, values for which are readily available.

Four of the epochs chosen are those said by Milankovitch to correspond with the Günz, Mindel, Riss and Würm glaciations: they are typical of years with very low amounts of summer radiation. The fifth epoch for which temperatures have been calculated is the one which is said to correspond with the 'climatic optimum', a period of high temperatures which immediately followed the retreat of the ice after the Würm glaciation; this epoch is typical of high summer radiation. The values entered in Table III are the differences between the January, July and mean annual temperatures to-day and the corresponding temperatures in the specified years; values are given for each of the six latitudes for which Milankovitch gives radiation data.

Examining the values entered in the upper half of Table III, we see that the changes in the mean temperature of the year (the third column in each group) are of different sign for latitudes below latitude 43° from those for high latitude. In the four glacial epochs the higher latitudes were colder than at present and the lower latitudes warmer, while the reverse was the case for the climatic optimum; this is because the inclination of the earth's axis was less than at present in the former cases and greater in the latter.

The effect of changes in the eccentricity of the orbit and the longitude of the equinox is to produce warmer summers and colder winters or vice versa without altering the temperature of the year as a whole. This is clearly seen in the columns headed January and July, in which the increase in the one is balanced by the decrease in the other when the change in the year as a whole, due to the inclination of the axis, is taken into account. In each of the glacial epochs the summer temperatures are lowered and the winter temperatures raised, the reverse being the case for the climatic optimum.

We have now to examine whether the changes of temperature entered in Table III are sufficient to account for the climatic changes which are ascribed to them. We will consider the climatic optimum first.

It will be remembered that the chief evidence for warmer conditions than at present immediately after the retreat of the ice was the extension of the oak, the maple, the hazel and the birch to greater heights on the mountains of Scandinavia than those where they live to-day. With July temperatures in Scandinavia between five and six degrees higher than to-day this seems to be satisfactorily explained; but it will be noticed that the January temperatures were

between four and six degrees lower. Whether these low winter temperatures are significant I have not seen discussed, and my own knowledge does not allow me to decide; but you as botanists will know.

Turning now to the conditions during the glacial epochs, the evidence is more conclusive. Let us take the values entered in Table III under Riss I. This was the epoch with the greatest extremes of radiation throughout the whole 600,000 years under consideration. We see that according to Milankovitch's data the July temperature was lowered $5\frac{1}{2}^\circ$ C. in latitude 55° N. and the January temperature raised by $4\frac{1}{2}^\circ$ C., the annual temperature being about half a degree lower than to-day. Now the July temperature between 40° N. and 80° N. decreases almost linearly with latitude at a rate of approximately 5·5° C. for 10° of latitude. Thus the summer temperature in latitude 55° N. at the peak of the Riss glaciation according to these calculations was the same as at present in latitude 65° N.; but in the Riss glaciation latitude 55° N. was heavily glaciated in North America and in Europe, but there is no approach to glaciation anywhere on latitude 65° N. at present. The conditions were even less favourable for glaciation in the other epochs assigned to the Günz, Mindel and Würm glaciations.

It is the generally accepted opinion that the cold conditions which gave rise to the ice sheets in high northern latitudes extended right to the equator. This would be very unlikely, as Penck (1938) points out, if the mean annual temperature of equatorial regions were raised as is shown in Table III.

There can be little doubt that the temperature changes calculated by Milankovitch's formulae as given in the upper half of Table III are quite insufficient to explain the conditions of the Ice Age, but it is easy to show that Milankovitch's temperature changes are about four times too large, and when the true changes are calculated they are seen to be quite insignificant from a climatic point of view.

This is not the place to undertake a critical examination of Milankovitch's mathematical treatment of the problem; but it is important that the weakness of his treatment should be set out so that palaeontologists and others who do not usually read mathematical treatises may form their own judgement.

Milankovitch works entirely from first principles. He considers a land surface (his equations do not hold for a water surface) and then he considers what happens to the solar energy which falls on the upper atmosphere. In his calculations he has to make certain assumptions; amongst these are (*a*) that there is no horizontal motion of the air, so that all the energy brought into a specified region by solar radiation leaves that region as terrestrial radiation; this

assumption we know is wrong, for it neglects the heat brought into the region or extracted by the winds ; in high latitude this energy is approximately equal to that brought in by solar radiation. He also assumes (*b*) that the atmosphere absorbs all long waves radiation equally ; and (*c*) proportionally to the mass of air traversed. We know that (*b*) is not even approximately correct, while (*c*) is wrong because it is the water-vapour and not the air which absorbs long wave radiation. For these reasons his calculated value of the relationship between temperature and radiation cannot be correct. Let us for a moment, however, assume that his values are correct, we see at once that as his calculations are based on a land surface they cannot apply to a water surface. That this is so is seen at once when we apply the changes in summer and winter temperatures given in Table III for a given latitude to the sea in that latitude. Take, for example, latitude 55° N. ; for this latitude at Riss I the summer temperature is reduced 5·4° C. and the winter temperature raised 4·6° C. If now we apply these values to the North Atlantic in latitude 55° N., where the summer temperature is now 12° C. and the winter temperature 6° C., we see that the winter temperature is brought above the summer temperature, which is absurd. The values given in Table III can therefore, if correct, be applied only to the land in the various latitudes and are too large when applied to the latitude as a whole, and still more so to ocean regions. Now it is interesting to note that the Pleistocene glaciation was at its maximum around the Atlantic Ocean ; just where the radiation would be least effective.

Milankovitch's solution of the problem has not succeeded because he has tried to calculate the actual change of temperature due to a change of radiation. This involves the absolute values of the constants he uses and they are not known. The problem can, however, be solved in a simple and satisfactory way by a different treatment.

Every place on a given latitude receives the same amount of solar radiation during the summer and during the winter ; that is, the annual range of radiation is the same at all places on the same latitude. Yet one place has a large annual range of temperature and another a small annual range. These variations are due to differences in the local conditions : the nearness to the sea, the type of surface, the prevailing winds, the amounts of cloud etc. It is a reasonable assumption that if the annual range of radiation of a latitude changed the range of temperature at each place on the latitude would respond but unequally : a place with a large annual range of temperature would have its temperature range increased

more than one with a small annual range. As a first approximation we may say that the temperature at all places on the same latitude would be increased or decreased by a given change of solar radiation in direct proportion to its annual range of temperature.

With these considerations as a basis and using Milankovitch's radiation data I have calculated the temperature changes given in the lower half of Table III *. The values give the change of the January, July and annual temperatures averaged over the stated latitudes. They are calculated by using the mean annual range of temperature for the latitude derived from the values of the January and July temperatures given in Table I. It is clear that places on or near the sea will have smaller ranges of temperature than the mean of the latitude and places inland will have larger ranges ; but in no latitude is the greatest actual range of temperature much more than twice the mean range for the latitude and on most latitudes much less. The changes of temperature given are, therefore, typical of the latitudes ; but they may require to be doubled in exceptional cases if the actual change for a locality is required, for example, in the middle of Asia.

It will be seen at once that these values are much less than those calculated by Milankovitch. The changes in the summer and winter values are all less than 2° C., and the changes in the annual values are all less than half a degree Centigrade except in the highest latitudes, where they may approach 1°.

Changes in temperature of these amounts can have little climatic significance, and certainly cannot have caused the large climatic changes which occurred in the Pleistocene Period.

It should be noticed that Table III contains the maximum changes in radiation due to changes in the earth's orbit which have occurred in the last 600,000 years, during which time the factors determining the orbit have gone through all their changes several times. We can therefore say that the changes of temperature which can be brought about by changes in the earth's orbit are of the order of 1° C. and seldom exceed this amount in any part of the world.

In view of these calculations I think we are justified in saying that there is no relationship between the zig-zags on the curve of summer radiation and the glacial and interglacial epochs of the Pleistocene Period ; and, further, that the changes of solar radiation due to changes in the earth's orbit are always too small to be of practical importance.

* The method of calculation is set out in detail in an appendix, p. 216.

Solar Theory.

(Changes in the Energy of the Sun.)

There has always been a reluctance amongst scientists to call upon changes in solar radiation (other than those associated with changes in the earth's orbit) to account for climatic changes. The sun is so mighty and the radiation emitted so immense that relatively short period changes, periodic or otherwise, have been almost unthinkable. The failure to find an adequate cause for the changes of climate in the earth itself has forced a reconsideration of extra-terrestrial causes.

Penck, than whom there is no more experienced and trusted worker in this field, is convinced that the Pleistocene Ice Age was accompanied by a general lowering of the temperature of the earth, and that the most probable cause of this change was a temporary decrease in solar radiation. At first he considered that in Europe a fall of temperature of 2 or 3° C. would be sufficient (Penck, 1906) ; but in more recent work he has increased this estimate to 8° C. (Penck, 1936). He bases his opinion chiefly on a lowering of the snow-line in all parts of the world, including equatorial regions, during the Ice Age, which he considers was unaccompanied by an increase of precipitation and therefore must have been due to a general lowering of the temperature (Penck, 1928).

Such a general lowering of the temperature cannot be explained by a change in the earth's orbit, for, as we have already seen, the only factor which changes the total radiation of a circle of latitude is the inclination of the earth axis to the ecliptic, and that always produces the opposite effect in equatorial and non-equatorial regions.

At first sight such a general lowering of the temperature, brought about by a decrease in solar energy, appears a simple and satisfying explanation. But there are difficulties. Decreased solar energy means a decrease in the difference between the amount of radiation received in equatorial and polar regions, resulting in a decrease in the general circulation of the atmosphere ; this, together with the lower temperature, leads to a decrease in the amount of water evaporated from the oceans. As the rainfall (including snow) balances the evaporation there must have been a general decrease in the precipitation. Penck (1928) recognizes this and believes that there is evidence, both in the Alps and in the Great Lake Basin in N. America, that the precipitation during the glaciation was certainly not more than at present—and possibly less.

So far as one can judge this does not apply in Greenland. The outflow of ice from Greenland was several times greater

during the Ice Age than at present, as is clear from the shape of the glacier valleys and other signs of increased thickness of the ice. As the greater part of Greenland, certainly that part which supplied the glaciers, is now well above the snow-line, greater outflow of ice can only have been brought about by increased precipitation. Lower temperatures would, of course, have reduced the evaporation from the ice fields; but no one supposes that this alone could have produced the greatly increased flow of ice. Similar conclusions, that the increased glaciation necessitated increased precipitation and not a mere fall of temperature, have been reached by many workers in fields outside Europe, in particular by von Ficker (1933) in his study of the Pleistocene glaciation of the Pamir Mountains, and by Meinardus (1925 and 1928) in his study of the water-balance in the Antarctic under present conditions and during the last Ice Age.

In most cases it is impossible to say definitely that the development of the ice could not have been the result of a general decrease in temperature, even accompanied by some decrease of precipitation; but in the case of the Antarctic Meinardus has been able to do this with mathematical certainty. This result is so important for all theories of climatic change that I should like to reproduce Meinardus's demonstration here, but as that would take too much time I must confine myself to sketching out the lines of his reasoning.

Meinardus imagines an open fence built up along the edge of the Antarctic continent reaching from the ground to the top of the atmosphere; it would go approximately along the circle of latitude 65° S. Through this fence at ground-level there is a steady outflow of ice; above ground-level air flows inwards and outwards. The air which goes in is warm and carries a certain amount of water-vapour, the air which comes out is exactly the same in amount, but it is colder and therefore carries less water-vapour; thus the interchange of air through the fence results in a certain amount of water being left behind. As the temperature within the fence is everywhere and at all times below the freezing-point, this water can remain behind only in the form of ice. It is this ice which flows out at ground-level, and therefore the total outflow of ice is on the average equal to the water-vapour left behind by the air which flows into and later out of the fence.

Now all explorers in the Antarctic have reported evidence of a much greater thickness of ice in relatively recent times from a geological point of view. A greater thickness of ice all over the Antarctic means an increased outflow of ice through our fence. Meinardus estimates that at its maximum the *outflow of ice* was at least double its present value and possibly three times. This increased outflow can only have been

caused by the incoming and outgoing air leaving more water-vapour behind in exactly the same proportion as the outflow of ice was increased.

Now the amount of water left behind depends on three factors only : (*a*) the amount of air which enters and leaves the fence ; (*b*) the amount of water carried in by a unit of air ; and (*c*) the amount of water carried out by a unit of air. The first of these obviously depends on the intensity of the general circulation of the atmosphere, and it can easily be shown that (*b*) and (*c*) depend mainly on the temperature of the in-going and out-coming air respectively, the possible changes in the relative humidity being too small to be important. Meinardus then shows, by an ingenious discussion in which he considers all possible combinations of air motion and temperature, that an increased outflow of ice can only be brought about by an increase in both the general circulation of the atmosphere and the mean annual temperature. He found that an increase of temperature of 5° C. and an increase in the wind velocity of 24 per cent. would produce a twofold outflow of ice.

If the temperature of the world during the last ice age had been reduced by 8° C., as suggested by Penck, the winds in and out of the Antarctic would have had to be increased by no less than four times to produce a twofold outflow of ice. Such a great increase in wind strength is in itself highly improbable ; but general meteorological theory shows that it would be quite impossible ; for as the temperature of polar regions depends largely on warm air brought from lower latitudes any increase in the flow of air into the Antarctic would lead to higher temperatures.

There can now be no doubt that at the maximum of the glaciation of the Antarctic the temperature was higher and the general circulation of the atmosphere increased. These conditions are quite inconsistent with a general lowering of the temperature of the world as a whole, due to a decrease in solar radiation. Against this it may be said that the conditions in the Antarctic are not typical of the rest of the world, or as Penck (1928, p. 83) suggests the maximum of the glaciation of the Antarctic may not have coincided with the maximum of the glaciation of the northern hemisphere, but with the post-glacial warm period, which we now call the climatic optimum. In any case the results found for the Antarctic and the opinion expressed by many glaciologists that there is evidence of increase of precipitation during the Ice Age in many parts of the world make us pause before accepting Penck's solution of the problem and ask whether there is not another solution which does not involve a decrease in solar radiation ?

It is agreed by everyone that glaciation would increase (*a*) if the temperature decreased while the precipitation remained the same, and (*b*) if the precipitation increased without any change of temperature. But are these relationships possible ? We have seen that for the Antarctic they are not, for we have shown that a decreased temperature can only produce the same precipitation if the interchange of air increases, and that is not consistent with a lower temperature. But has this result a general application or is it true of the Antarctic only because of its peculiar geographical position ?

While working on a meteorological problem, without any thought of this particular question, I was led to the conclusion that the conditions which we have found for the Antarctic are true for the world as a whole, and that the glacial epochs were the consequence of an increase and not a decrease in the solar radiation.

The argument can be stated very simply. With the present amount of solar radiation the atmosphere has taken up a steady state which results in the same amount of radiation being returned to space in the course of a year as is received from the sun. This balance is affected in three ways : (*a*) by the temperature of the surface, (*b*) by the temperature of the upper atmosphere, and (*c*) by the amount of cloud, for by reflexion thick clouds return 78 per cent. of the solar radiation which falls upon them. If the solar radiation changes (*a*) and (*c*) certainly change. The process by which this comes about is easily seen. Let us assume that the solar radiation increases ; this will cause an increase of temperature of the surface. But the rise of temperature is not uniformly spread over the surface : the temperature at the equator rises more than the temperature at higher latitudes. This increases the general circulation of the atmosphere, which depends on the temperature gradient from the equator to the poles. The increased temperature and the increased air motion results in increased evaporation from the oceans. This increased evaporation leads to greater cloud formation and more precipitation—in fact, the process continues until the increased precipitation balances the increased evaporation. But the increased cloud amount reflects a greater proportion of the incoming solar radiation, so there is less radiation received by the surface, and the surface temperature does not have to rise so much to balance the radiation received. There is every reason to believe that the change in the cloud amount is the predominating factor in the regulation of the temperature of the atmosphere. The atmosphere appears to act as a great thermostat, keeping the temperature nearly constant by changing the amount of cloud. Nevertheless,

an increase of solar radiation must produce some increase of temperature, if only to cause the necessary increase in the cloud amount by increasing the evaporation.

We are not able to calculate exactly what would be the change in temperature and cloud amount for a given change in solar radiation; but we are able to set limits. If solar radiation increased by 10 per cent., and there was no change in the amount of cloud, the mean temperature of the surface would rise by 16° C. If, on the other hand, the temperature of the surface remained unchanged the balance would be restored if the cloud amount increased from its present value of 5·4 (10 = overcast) to 6·6. There can be little doubt that this increase in cloud amount would be reached with a much less increase of temperature than 16° C., therefore the increase of cloud is the chief factor in effecting the balance of radiation, and the temperature of the surface undergoes a relatively small change.

In non-glaciated regions as the solar radiation increases there will be an increase of cloud with some increase of temperature. Unfortunately, there is no definite relationship between the amount of cloud and the amount of precipitation, except that as the increase of cloud is the result of increased evaporation there must be a corresponding increase in precipitation. The temperature of a cloudy place is more equitable than one with less cloud. The result is that although the mean temperature will rise somewhat the extremes may be reduced locally. This will be especially the case in the summer months when the increase of cloud due to increased solar radiation is at its maximum. Thus in non-glaciated regions the summer will tend to be cooler and the winter warmer, and there will be increased precipitation.

In glaciated regions and regions with mean annual temperatures near the freezing-point, the increased precipitation and the decreased sunshine in the summer will tend to the accumulation of snow. The snow-line will be lowered, and in spite of the increased temperature the glaciers will grow. The effect of the increased radiation on glaciation will be different in different localities and geographical positions. In regions such as the Antarctic, inner Greenland and high mountains, where the temperature all the year round is below the freezing-point, the increased precipitation will certainly lead to increased outflow of ice, which will overrun the low lands and feed the ice sheets on the continents.

The ice which enters the sea from these regions will have a large effect on remote regions, and there can be little doubt that it was the flow of ice into the North Atlantic from the Arctic basin and from the mountains of Greenland and Norway which lowered the temperature in Europe and North America

and caused the asymmetrical position of the Pleistocene ice cap in the northern hemisphere.

With continued increase of radiation the mean temperature will increase : the snow-line will rise and the forward edges of the ice sheets on the continents will be melted back. The polar regions will continue to pour out more ice ; but there will be a steady decrease in the area glaciated. The climate of the regions recently glaciated will have a higher mean temperature than at present ; but there will be so much cloud and rain that there will be little difference between summer and winter—the winters especially being less severe than at present.

If the radiation now decreases the whole process is gone through in the reverse order : the glaciers extend and the ice sheets reappear and then retreat as the precipitation decreases until we return to the conditions of to-day, when the glaciers are confined to the high mountains and the ice sheets have disappeared except from Greenland and the Antarctic.

During these periods of increase and decrease of radiation non-glaciated regions have experienced slight changes of temperature and large changes of rainfall. Whereas the glaciation retreated for a period when the radiation was at its maximum, so producing two glacial epochs, there will have been no such break in the increase of the rainfall.

When the glaciation first appeared in high latitude the rainfall in non-glaciated regions was already heavy as compared with present conditions. The pluvial period had commenced and continued to increase until it reached its maximum in the epoch between the two glaciations. The rainfall then decreased ; it was still heavy when the ice finally commenced to retreat, and with the disappearance of the ice present conditions were restored. Thus a pluvial period embraces two glacial epochs, and is at its maximum simultaneously with the interglacial epoch which separates them.

This appears to me the only way in which we can reconcile the fact that higher temperatures and greater general circulation of the atmosphere are absolutely essential to produce increased outflow of ice in the Antarctic. It explains many of the details of the climatic changes during the Pleistocene Ice Age (Simpson, 1934) with its four glacial epochs and great river flow in the interglacial between the last two glacials.

It is admitted that this explanation is largely qualitative and that numerical values cannot be given at present. It is, however, susceptible to proof or disproof when geologists have succeeded in correlating the pluvial periods of non-glaciated regions—such as North America and Africa—with the advances and retreats of the ice in the glaciated regions. If it is found that there was one pluvial period for each glaciation, as is

generally held, or that the glacial epochs were relatively dry and the pluvial periods were confined to the interglacial epochs, as held by Penck, the explanation I have given must fall, for it requires that there should be one pluvial period embracing the Riss and the Würm glacial epochs with its maximum in the interglacial between them.

Summary.

Three possible causes of change of climate are discussed :

(*a*) The effect of the distribution of land and water is examined, and it is found that the mean temperature and mean rainfall of zones is unaffected by the distribution of land and water ; but that large difference in the climate of localities may be brought about by redistribution of land and water, chiefly in the extremes of temperature and in the rainfall. The changes of climate during the Pleistocene Period could not have been caused by changes in land and water.

(*b*) The effect of changes in the elements of the earth's orbit is shown to be so small that the mean annual temperatures cannot anywhere be affected by more than one- or two-tenths of a degree Centigrade, while the temperature of the warmest month and coldest month can only be affected by as much as 2° C. in extreme cases in high latitude.

(*c*) An increase in solar radiation produces an increase in temperature, in cloud amount and in precipitation, and a decrease produces the reverse effects. The large changes in climate during the Pleistocene Period are probably due to changes in solar radiation ; but it is not yet clear whether the glacial epochs were caused by an increase or decrease of solar radiation.

Appendix.

Revised method of calculating the change of temperature due to change in solar radiation.

We assume that at any place the annual range of temperature, y, varies in the same proportion as the annual range of radiation, R, i.e.

$$\frac{R'}{R} = \frac{y'}{y} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (1)$$

in which the undashed letters refer to the present time and the dashed letters to some specified previous year.

As the annual variations of both radiation and temperature

follow very closely a sine curve there is a constant ratio between the range defined (*a*) as the difference between the mean of the summer half year and the mean of the winter half year, and the range defined (*b*) as the difference between the mean of the month at the maximum and the mean of the month at the minimum. We may therefore in equation (1) use either of the two ranges (*a*) or (*b*). In practice we have in Milankovitch's tables values of the radiation given as the mean of the summer and mean of the winter half years, hence for radiation it is convenient to use range (*a*); for temperature, on the other hand, we have values for January and July and not for the mean for the winter and summer half years, hence for temperature it is convenient to use range (*b*). We can now define R as the difference between the radiation in the summer and winter half years, i.e. $R=Q_s-Q_w$ and y as the difference between the mean temperature of the warmest summer month and the mean temperature of the coldest winter month, i.e. $y=T_s-T_w$

We will also write

$$\begin{array}{lll} \Delta T_s & \text{for} & T_s'-T_s, \\ \Delta T_w & ,, & T_w'-T_w, \\ \Delta Q_s & ,, & Q_s'-Q_s, \\ \Delta Q_w & ,, & Q_w'-Q_w, \\ \Delta R & ,, & R'-R, \\ \Delta y & ,, & y'-y, \end{array}$$

in which, as before, the undashed letters refer to the present time and the dashed letters to the specified previous year.

From (1) we have

$$y'=y\frac{R'}{R}.$$

As y, R' and R are all known we can write down at once the value of the temperature range in the specified previous year. But this gives us only the difference between the summer and winter temperatures, and does not specify what those temperatures were. If the change in radiation had been equally divided between the summer and the winter we should naturally divide the change in the temperature range equally between the summer and the winter temperatures. In general the changes in the radiation are not the same in the summer and the winter, and it seems reasonable to divide the change in the temperature range between the summer and the winter in the same proportion as the change in radiation is divided between summer and winter.

Hence we have

$$\frac{\Delta T_s}{\Delta T_w}=\frac{\Delta Q_s}{\Delta Q_w}. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (2)$$

From (1) we have

$$\frac{R+\Delta R}{R}=\frac{y+\Delta y}{y},$$

i.e.

$$\frac{\Delta R}{R}=\frac{\Delta y}{y};$$

hence

$$\Delta y=\frac{y}{R}\Delta R. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (3)$$

Further, by definition,

$$\Delta y=\Delta T_s-\Delta T_w.$$

Substituting for ΔT_s from (2) we have

$$\Delta y=\frac{\Delta Q_s}{\Delta Q_w}\Delta T_w-\Delta T_w$$

$$=\Delta T_w\left(\frac{\Delta Q_s-\Delta Q_w}{\Delta Q_w}\right) \quad . \quad . \quad . \quad . \quad (4)$$

From (3) and (4) we have

$$\frac{y}{R}\Delta R=\Delta T_w\frac{\Delta R}{\Delta Q_w},$$

i.e.

$$\Delta T_w=\frac{y}{R}\Delta Q_w \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (5)$$

Similarly, we have

$$\Delta T_s=\frac{y}{R}\Delta Q_s. \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (6)$$

From equations (5) and (6) we can write down the changes in the summer and winter temperatures as we know y, R, ΔQ_w and ΔQ_s.

Example.—To find the temperatures of the warmest and coldest months at a place in latitude 65° N. in the year 116·1 thousand years ago (this is the year when Würm I was supposed to be at its maximum), it being given that the temperature at the specified place at present is −21·2° C. in January and 10·7° C. in July (the mean range for latitude 65° N. at present).

We have

$y=31{\cdot}9$ from $10{\cdot}7°+21{\cdot}2°$.
$R=11204$ „ Milankovitch's Table 14.
$\Delta Q_s=-553$ from Milankovitch's Table 15.
$\Delta Q_w=+299$ from Milankovitch's Table 15.

Therefore

$$\Delta T_s=\frac{31{\cdot}9\times-553}{11204}=-1{\cdot}58, \text{ i.e. } T_s=19{\cdot}7-1{\cdot}6=9{\cdot}1° \text{ C.},$$

and

$$\Delta T_w=\frac{31{\cdot}9\times299}{11204}=+{\cdot}85, \text{ i.e. } T_w=-21{\cdot}2+{\cdot}8=-20{\cdot}4° \text{ C.}$$

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